LES PRATIQUES SILVICOLES CONTRÔLENT LA CAPACITÉ COMPÉTITIVE DES ARBUSTES ERICACÉES BORÉALES: INTERACTIONS AVEC LE REGIME CLIMATIQUE ET LE DEPOT GEOLOGIQUE

SILVICULTURAL PRACTICES CONTROL THE COMPETITIVE ABILITY OF BOREAL ERICACEOUS SHRUBS: INTERACTIONS WITH CLIMATE REGIME AND GEOLOGICAL DEPOSIT

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RÉSUMÉ

La forêt boréale est un biome qui a une distribution circumpolaire et offre un éventail de ressources économiques. La gestion forestière a pour tâche de assurer des forêts productives qui génèrent des sources de richesse tout en respectant l'écosystème forestier. Afin de remplir cette tâche, la gestion forestière doit développer un plan de gestion durable pour assurer l'avenir du régime de gestion forestière. Dans les forêts boréales d'épinettes noires (*Picea mariana* (Mill.) BSP) de l'est du Canada, des espèces d'arbustes éricacées telles que le laurier de brebis (*Kalmia angustifolia* L.) et le thé du Labrador (*Rhododendron groenlandicum* (Oeder) Kron & Judd) ont évolué entre différents mécanismes avec la croissance des semis de conifères et réduire la fertilité du site. Si elle est mal gérée, la compétitivité agressive des espèces d'éricacées pourrait compromettre une foresterie durable. Notre étude examine comment les caractéristiques compétitives des arbustes éricacés répondent à deux pratiques sylvicoles généralement pratiquées au Québec, Canada; éclaircie pré-commerciale (Chapitre 2) et scarification (Chapitre 3). De plus, partout au Québec, il existe des gradients de température et de précipitations, ainsi que des dépôts de sol différents. On pense que les arbustes éricacés favorisent les climats maritimes humides et les sites fertiles pauvres par rapport aux climats continentaux et aux sites fertiles riches. Par conséquent, ces facteurs peuvent interagir avec les deux pratiques sylvicoles pour contrôler la capacité compétitive des arbustes éricacés.

Au chapitre 2, nous nous intéressons à l'éclaircie précommerciale (ÉPC), une pratique sylvicole qui consiste à couper des arbres sélectionnés pour réduire la densité de l'étage supérieur dans la forêt. Cela augmente les ressources disponibles pour les tiges restantes, mais on craint que cette pratique ne favorise la propagation d'arbustes éricacés. Ainsi, nous avons examiné l'impact de L'ÉPC sur la propagation et la capacité competitive des arbustes

éricacés dans un climat continental par rapport à un climat maritime et avons étudié l'impact de l'ÉPC sur les dépôts de sol argileux fertiles vs dépôts de sol till pauvres en nutriments. Nous avons trouvé que la couverture totale d'arbustes éricacés augmentait sur les parcelles ÉPC par rapport aux parcelles témoins et qu'il y avait une plus grande couverture d'arbustes éricacés dans les sites à climat maritime par rapport aux sites à climat continental. En outre, nous avons trouvé une relation positive significative entre l'ouverture du couvert forestier et la couverture d'arbustes éricacés, la longueur du rhizome de *K. angustifolia* de l'année en cours, et le tanin condensé foliaire de *K. angustifolia* et les concentrations phénoliques totales. Les parcelles ÉPC sur des dépôts de till pauvres en nutriments avaient des rhizomes plus longs de *K. angustifolia* avec une masse spécifique de rhizome plus élevée. Sur les dépôts de till pauvres en nutriments, le sol minéralisable NH4 + -N était plus faible sous les arbustes de *K. angustifolia* que sous la mousse de plumes (*Pleurozium schreberi* spp.). Par conséquent, nous concluons que l'ÉPC augmente la propagation d'arbustes éricacés et que le degré de compétitivité des arbustes éricacés augmente dans un régime climatique maritime et dans des dépôts géologiques de till.

Au chapitre 3, nous nous concentrons sur la scarification, une pratique sylvicole post-récolte qui crée des tranchées pour améliorer le lit de semis des conifères plantés. De plus, cette pratique empêche les empiétements des arbustes éricacés au moment de la plantation des semis. Des études à long terme sur cette pratique sont essentielles pour déterminer l'efficacité de la scarification et plusieurs études ont montré que la scarification améliore la croissance des conifers. Cependant, la plupart des études se concentrent principalement sur la croissance des conifères et négligent une étude approfondie des espèces d'arbustes éricacées. En outre, la plupart des études ne comparent pas les effets de la scarification dans des climats contrastés. Notre étude se concentre sur la compétitivité des arbustes d'éricacées 16 ans après le traitement dans un climat maritime et continental. Nous avons trouvé que la scarification réussissait à réduire l'empiétement à long terme des arbustes éricacés sur les deux sites. Les parcelles scarifiées avaient une couverture arbustive moins éricacée et des rhizomes plus

courts de *K. angustifolia* de l'année en cours par rapport aux parcelles non scarifiées. Cependant, il existait de plus grandes différences de traitement dans le climat maritime, notamment une plus faible ouverture de la canopée, de plus faibles concentrations phénoliques folaires de *K. angustifolia*, une plus faible efficacité d'utilisation de l'azote foliaire de *K. angustifolia* et une plus grande quantité d'azote foliaire de *K. angustifolia* sur les parcelles scarifiées par rapport aux parcelles non scarifiées. Par conséquent, nous concluons que la scarification continue d'être efficace 16 ans après le traitement et continue de réduire la compétitivité des arbustes éricacés, mais pourrait être plus bénéfique dans les climats maritimes que dans les climats continentaux.

Mots clés: épinette noire, forêt boréale, régime climatique, arbustes éricacés, éclaircies précommerciales, scarification, dépôt de sol, foresterie durable

SUMMARY

The boreal forest is a biome that has a circumpolar distribution and offers an array of economic resources. Forest management has the task of ensuring productive forests that generate wealth sources while respecting the forest ecosystem. In order to fulfill this task, forest management must develop a sustainable management plan to ensure the future of the forest management regime. In boreal black spruce (*Picea mariana* (Mill.) B.S.P.) forests of Eastern Canada, ericaceous shrub species such as sheep laurel (*Kalmia angustifolia* L.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) have evolved various mechanisms that interfere with conifer seedling growth and reduce site fertility. If managed improperly, the aggressive competitiveness of ericaceous species could compromise sustainable forestry. Our study examines how competitive traits of ericaceous shrubs respond to two silvicultural practices commonly performed in Quebec, Canada; pre-commercial thinning (Chapter 2) and scarification (Chapter 3). Furthermore, across Quebec there are temperature and precipitation gradients as well as differing soil deposits. It is believed that ericaceous shrubs favor wet maritime climates and poor fertile sites relative to continental climates and rich fertile sites. Therefore, these factors may interact with the two silvicultural practices in controlling the competitive ability of ericaceous shrubs.

In Chapter 2, we focus on pre-commercial thinning (PCT) which is a silvicultural practice that cuts selected trees to reduce the density of the overstory in the forest. This increases resources available to the remaining stems, however, there are concerns that this practice is conducive to the spread of ericaceous shrubs. Thus, we examined how PCT impacts the spread and competitive ability of ericaceous shrubs in a continental climate *vs*. maritime climate and studied the impact of PCT on fertile clay deposits *vs*. nutrient poor till deposits. We found that the total cover of ericaceous shrubs increased on PCT plots compared to

control plots and that there was a higher cover of ericaceous shrubs within the maritime climate sites compared to the continental climate sites. Additionally, we found a significant positive relationship between canopy openness and ericaceous shrub cover, *K. angustifolia* current-year rhizome length, and *K. angustifolia* foliar condensed tannin and total phenolic concentrations. PCT plots on nutrient poor till deposits had longer *K. angustifolia* rhizomes with a higher specific rhizome mass. Also on the nutrient poor till deposits, soil mineralizable NH_4^+-N was lower under *K. angustifolia* shrubs than under feather moss (*Pleurozium schreberi* spp.). Therefore, we conclude that PCT increases the spread of ericaceous shrubs and that the degree of competitiveness from ericaceous shrubs increases in a maritime climate regime and on till geological deposits.

In Chapter 3, we focus on scarification which is a post-harvest silvicultural practice that creates trenches to improve the seedling bed for planted conifers. Additionally, this practice prevents encroachment from ericaceous shrubs at the time seedlings are planted. Long-term studies on this practice are essential to determine the effectiveness of scarification and several studies have shown scarification improves conifer growth. However, most studies focus primarily on conifer growth and neglect an in depth study of ericaceous shrub species. Furthermore, most studies do not compare the impacts of scarification in contrasting climates. Our study focuses on the competitiveness of ericaceous shrubs 16-years after treatment within a maritime climate and a continental climate. We found scarification successfully reduced the long-term encroachment of ericaceous shrubs in both sites. Scarified plots had less ericaceous shrub cover and shorter *K. angustifolia* current year rhizomes compared to non-scarified plots. However there were greater treatment differences in the maritime climate including, lower canopy openness, lower *K. angustifolia* foliar phenolic concentrations, lower *K. angustifolia* foliar nitrogen-use efficiency, and higher *K. angustifolia* foliar nitrogen on scarified plots compared to non-scarified plots. Therefore, we conclude scarification continues to be effective 16-years after treatment and continues to

reduce the competitiveness of ericaceous shrubs, but may be more beneficial in maritime climates compared to continental climates.

Key words: black spruce, boreal forest, climate regime, ericaceous shrubs, pre-commercial thinning, scarification, soil deposit, sustainable forestry

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LIST OF ABBREVIATIONS

AAC = Annual allowable cut

MFFP = Ministry of Forests, Fauna, and Parks

PCT = Pre-commercial thinning

CPRS = La coupe avec protection de la régénération et des sols

N = Nitrogen

SRM = Specific rhizome mass

SRL = Specific rhizome length

SLA = Specific leaf area

C:N = Carbon to nitrogen ratio

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CHAPTER 1

GENERAL INTRODUCTION

Boreal forests encompass a vast area including dominating the landscape throughout Scandinavia, Alaska, Canada, and Russia. These forests serve a vital role as sinks or sources of atmospheric CO_2, provide recreational opportunities, and are an important economic resource from harvesting timber (Anderson, 1991; Goodale et al., 2002). Therefore, management of these forests have pronounced regional and global ramifications and sustainable management is vital for the continued productivity of these forests.

Quebec, Canada is dedicated to practicing sustainable forestry through the governing body of the Ministry of Forests, Fauna, and Parks (MFFP) (previously the Ministry of Natural Resources and Fauna). Throughout the years, Quebec's forest management regime has undergone several transformations in undertaking new forest-related issues (whether social, environmental or economic), adopting new management approaches (such as introducing the concept of ecosystem-based management), and amending legislation and regulations. A significant event, within the history of the forest management regime, was the formation of the Coulombe Commission (Commission d'étude sur la gestion de la forêt publique québécoise) in 2004, which conducted an exhaustive examination of Quebec's forest regime. One of its main "recommendations" was the appointment of a Chief Forester who would have a central role in the forest management strategy (Commission d'étude sur la gestion de la forêt publique Québécoise, 2004).

The Chief Forester is responsible for assessing the impacts of the current management strategy that may affect harvest levels. This includes determining the maximum amount of annual timber to be harvested within a given time frame, without diminishing the productive capacity of the forest (Bureau du forestier en chef, 2013). This allowable cut must maintain other forest management objectives such as sustainable forest management objectives as well as the natural dynamics of forests such as composition, age structure, and multiple diversified uses (Bureau du forestier en chef, 2013). The annual allowable cut (AAC) is then used as a base for strategic plans and to forecast the forestry operations to be carried out over a five-year time frame (Ministère des Ressources naturelles et de la Faune, 2008).

The AAC incorporates the most current knowledge about the state of the forest and represents the annual productive capacity of the forest. This is a central concern of sustainable forest management because harvest rates cannot exceed the annual productive capacity of the forest in order to maintain sustainable yields. A part of the calculation includes taking into account invasion by ericaceous shrubs. It has been observed that after forest disturbances such as forest fires or clear cutting, ericaceous shrubs rapidly proliferate by rhizomatous growth through the organic soil layer most notably by Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), sheep laurel (*Kalmia angustifolia* L., referred from here as *Kalmia*), and *Vaccinium* spp. (Mallik, 1993). Sites invaded by ericaceous shrubs have experienced regeneration failures or decreases in conifer growth rates, known as "growth check" (Damman, 1971; Titus et al., 1995; Lebel et al., 1998). The calculation takes into account up to a 25 year forest rotation delay from invasion by ericaceous shrubs, however in extreme cases, retrogressive succession can occur in which conifer stands transform into ericaceous heaths (Bureau du forestier en chef, 2013; Royo and Carson, 2006). Several mechanisms have been proposed to explain ericaceous shrub domination of a site including direct and indirect competition for nutrients, most notably nitrogen (N). Thiffault et al. (2004) found *Kalmia* was able to uptake larger amounts of N

compared to black spruce (*Picea mariana* (Mill.) B.S.P.) due to a higher amount of root biomass and root surface area. Additionally, several indirect methods from allelochemical interference have also been proposed (Mallik, 1987; Yamasaki et al., 1998; Preston, 1999). Mallik (1987) found black spruce root growth was inhibited by extracts of *Kalmia* litter, while Yamasaki et al. (1998) suggested *Kalmia* phenols may reduce mycorrhizal colonization of black spruce seedlings.

Although allelopathic metabolites may contribute to the reduction in conifer growth, clearer evidence suggests condensed tannins produced by ericaceous shrubs give this species a greater advantage over conifers. Condensed tannins, a subset of phenolics, are carbon based polymers consisting of flavan-3-ols and have the capacity to bind to soil proteins to form tannin-protein complexes (Hättenschwiler and Vitousek, 2000; Kraus et al., 2003). These recalcitrant complexes prevent dissolved organic N within the forest floor from mineralizing into ammonium-N, which is the N source preferred by conifers (Joanisse et al., 2009). Additionally, black spruce specifically favors acquiring nitrogen within the organic soil layer, which coincides with the soil layer ericaceous shrub's extensive root network proliferates through. This further exasperates the difficulties of acquiring nutrients on sites dominated by ericaceous shrubs. (Strong and La Roi, 1983; Steele et al., 1997). This is evident from a study that showed a correlation between soil N-mineralization rates within the organic soil layer and black spruce growth which were lower on sites where *Kalmia* was maintained in comparison to sites where *Kalmia* was removed (Lebel et al., 2008). Furthermore, is has been demonstrated that *Kalmia* tannins reduce extracellular soil enzyme activity from tannins binding to and inhibiting soil enzymes, specifically ß-glucosidase and acid phosphatase (Joanisse et al., 2007). This presents another mechanism of *Kalmia* tannins reducing nutrient cycling rates. However, the reduction in nutrient cycling does not negatively affect N acquisition by ericaceous species as much as conifer seedlings. This advantage of ericaceous species over conifer seedlings in the acquisition of N is due to an association with ericoid mycorrhizae. Ericoid mycorrhizal extracellular enzymes break down

tannin-protein complexes and organic N for the obtainment of N by ericoid mycorrhizae. (Kraus et al., 2003; Bending and Read, 1996). Therefore, ericaceous shrub tannins negatively impact soil N-cycling which in turn prevent conifer regeneration as well as reduce conifer growth while ericaceous species proliferate. Only once conifers establish an extensive root network are they able to acquire adequate nutrients to surpass the threshold of the ericaceous shrub "growth check" (Bureau du forestier en chef, 2013).

According to the Bureau du forestier en chef (2013), a focus of the MFFP is maintaining the productivity of harvestable lands and counteracting the invasion of ericaceous shrubs. This management strategy is accomplished by limiting cutting practices that promote ericaceous shrub invasion, such as "La coupe avec protection de la régénération et des sols" (CPRS). Additionally in an attempt to counteract ericaceous shrub expansion, site preparation treatments are administered following harvests in areas at risk of regeneration failure or already experiencing invasion by ericaceous species. Scarification is a type of ground preparation performed post-harvest to promote the establishment of planted conifer seedlings. A machine mixes the organic and mineral soil horizons, often creating a trench of bare mineral soil (Fig. 1.1). This creates favorable safe sites for conifer seedlings to be planted within the trench. Additionally, the trench creates a buffer zone from encroaching ericaceous species, that propagate through the organic soil layer, and allows seedlings enough time to establish an adequate root system (Thiffault and Jobidon, 2006; Thiffault et al., 2005; Moroni et al., 2009; Bureau du forestier en chef, 2013). One of the benefits of this practice is that established seedlings will shade out understory shrub species, including ericaceous shrubs, over time, and thus reduce the competition for resources.

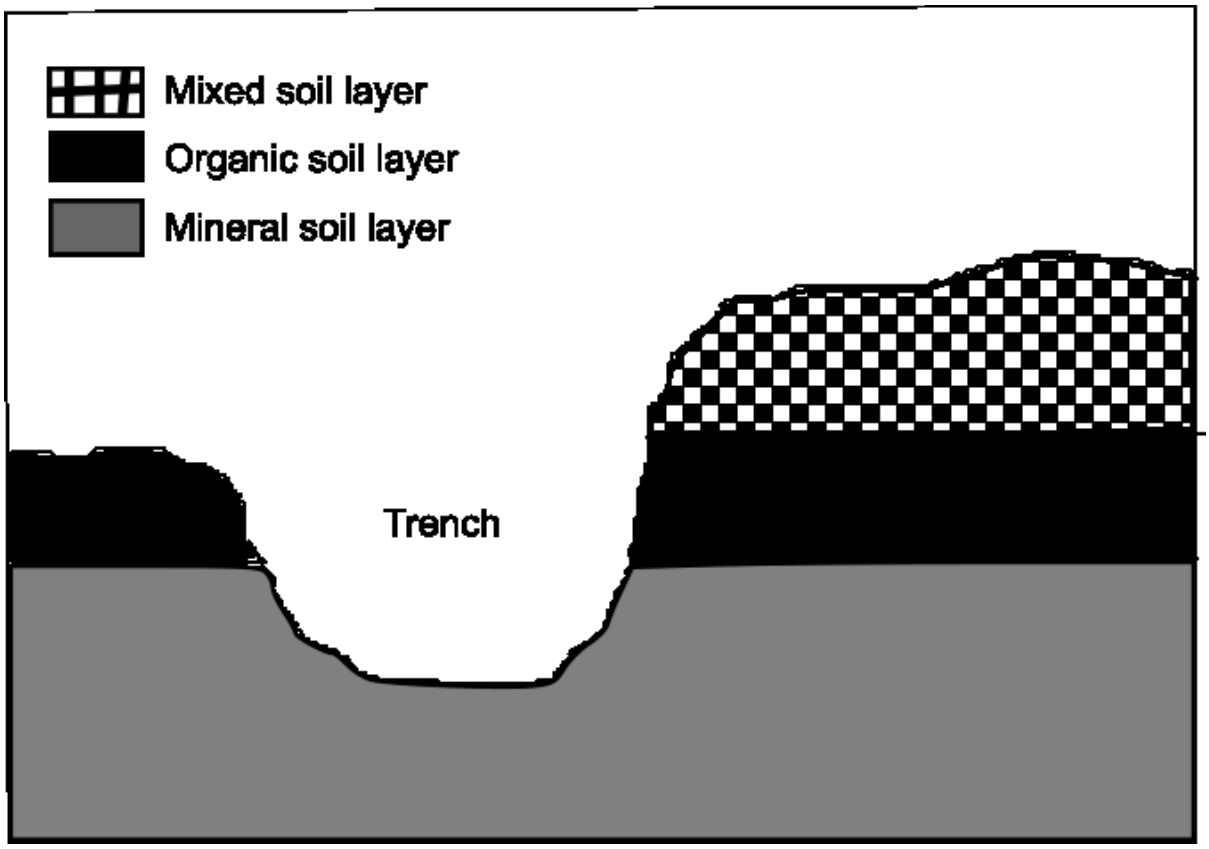

Figure 1.1 Scarification diagram from passive disc trenching. A mixture of organic soil and mineral soil is deposited to one side of the trench, creating a mixed soil layer overtop the organic soil layer.

The modeling approach taken by the Chief Forester to calculate the AAC will only hold true if current and past conditions reflect future conditions. Given the rate at which global changes are occurring, this assumption is somewhat tenuous. For this reason, a strategic project was proposed in 2014, with intentions to evaluate possible interactions between climate change and silvicultural treatments in controlling forest growth. The project was funded in 2015 by a National Science and Engineering Research Council of Canada (NSERC) Strategic Project Grant to collaborate multiple university research labs in eastern Canada, including the *Laboratoire des sols*-Université de Sherbrooke, with the MFFP. One

of the main objectives of the project was to create a model that would predict forest growth taking into account climate change predictions and silvicultural treatments. However, due to the nature of ericaceous shrubs competing with conifers such as black spruce and influencing forest growth, it was realized that the competitive nature of ericaceous species should also be taken into account. Thus, a study was proposed to examine the competitive ability of ericaceous species. I was recruited in 2016 to begin this project on the interactions between silvicultural treatment and climate regime and between silvicultural treatment and geological deposit in controlling the competitive ability of ericaceous shrubs. The study included sites throughout Quebec to distinguish different climate regimes as well as varying soil deposits. This study informed the MFFP and the Chief Forester of areas more at risk of conifer growth delays based upon the interactions that drive the competitiveness of ericaceous species. The project focused on two silvicultural practices, pre-commercial thinning (PCT) in Chapter 2 and scarification in Chapter 3.

PCT is a silvicultural practice performed 15 to 20 years after a harvest in densely regenerated forests. The objective of this practice is to increase the growth rate of selected trees by reducing stand density and removing non-crop tree species. This is to provide more resources to selected trees and shorten the forest rotation age. Thus, this practice increases the light availability to the understory, changing the closed canopy to a semi-open canopy. Additionally, the cuttings left on site produce an influx of down woody debris. The increase in light and organic material may favor ericaceous shrubs due to ericaceous species favoring semi-light environments and possibly preferring moist woody substrates (Huffman et al., 1994a; Huffman et al., 1994b, Messier, 1992). Performing this practice during each harvest cycle could increase the risk of invasion by ericaceous species. This consequently compromises sustainability. Additionally, the current forest management plan does not consider how the competitiveness of ericaceous shrubs may differ on contrasting site types. It has been suggested that ericaceous shrubs are more competitive on nutrient poor sites and in maritime climates that have an accumulation of lignin-rich organic soil (Prescott, 1995;

Damman, 1971; Meades, 1983; Huffman et al., 1994b; Titus et al., 1995). Therefore, the objective of this study was to test for interactions between PCT and climate regime, and PCT and soil deposit in controlling the competitive ability of ericaceous shrubs. We believe that ericaceous shrubs are more competitive in canopy gaps, in thick forest floors, and on nutrient poor soils. Therefore, PCT will increase ericaceous shrub competitive ability and this increase will be more pronounced in maritime climates and on nutrient poor till soil deposits compared to continental climates and on nutrient rich clay soil deposits.

As previously described, scarification is a process performed in areas with high risk of ericaceous shrub invasion or areas that have low conifer regeneration in order to promote conifer growth. The objective is to create favorable safe sites to allow conifers to adequately establish and shade out ericaceous shrubs over time. By reducing the available light to the understory, it is predicted that ericaceous shrub competitiveness will decrease. However, it is unknown at what stage shading effectively reduces ericaceous shrub competitiveness. Additionally, few studies have investigated ericaceous shrub response to scarification in contrasting climate regimes. Due to ericaceous shrubs potentially favoring maritime climates, forest management strategies may need to alter depending on location. Therefore, the objective of this study was to test for interactions between scarification and climate regime in controlling ericaceous shrub competitive ability. We believe that scarification accelerates canopy closure and that ericaceous shrubs are less competitive in thinner forest floors. Therefore, scarification will decrease ericaceous shrub competitive ability and this will be more pronounced in a continental climate than in a maritime climate.

CHAPTER 2

PRE-COMMERCIAL THINNING OF BOREAL BLACK SPRUCE STANDS MAY REDUCE LONG-TERM SITE FERTILITY BY INCREASING THE COMPETITIVE ABILITY OF ERICACEOUS SHRUBS: INTERACTIONS WITH CLIMATE REGIME AND GEOLOGICAL DEPOSIT

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2.1 Foreword

Chapter 2 focuses on the interactions between pre-commercial thinning (PCT) and climate regime and interactions between pre-commercial thinning and soil deposit in controlling the competitive ability of boreal ericaceous shrubs. Our study is one of the first to bring recognition to the potential risks to sustainable forestry from PCT that may create a more favorable growing environment for ericaceous shrubs. Additionally, our study is one of the first to examine rhizome growth of ericaceous shrubs in contrasting climates and soil deposits. Our study will aid science in better understanding ericaceous life history traits that drive its competitive nature. This in turn will lead to better forest management plans and decision making that support sustainable forestry practices. The co-authors of this article are Krista Reicis, Robert L. Bradley, Gilles Joanisse, Stephane Tremblay, Martin Barrette, Daniel Houle, and Amy Wotherspoon. Robert L. Bradley and Krista Reicis conceived the ideas of the project while all co-authors aided in the design and methodology. Krista Reicis and Amy Wotherspoon collected the field samples. Krista Reicis analyzed the data in the laboratory, with the aid of Gilles Joanisse, and performed the statistics. All co-authors contributed to the interpretation of the data. Krista Reicis and Robert L. Bradley led the writing of the manuscript and all co-authors gave final approval for publication. This manuscript will be submitted to the Journal of Applied Ecology.

2.2 Abstract

1. Ericaceous shrubs such as sheep laurel (*Kalmia angustifolia* L.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) have evolved various mechanisms that have shown to interfere with the growth of regenerating boreal conifers following major forest disturbance. Moreover, studies have shown that this phenomenon is exacerbated by moist (i.e. maritime) climate regimes and by low soil fertility.
2. Our study examined how pre-commercial thinning (PCT) of young black spruce (*Picea mariana* (Mill.) B.S.P.) stands, a common silvicultural practice, also impacts the spread and competitive ability of ericaceous shrubs. Furthermore, we examined how PCT affects the chemical quality of ericaceous shrub litter as well as soil nitrogen cycling. We compared these effects in moist maritime and drier continental climates. Within the continental climate, we compared these effects on fertile clay and on nutrient-poor till deposits.
3. The cover of ericaceous shrubs was higher in PCT than in control plots in all three site types. On nutrient poor till deposits (in both maritime and continental climates), the current year rhizome length and specific rhizome mass of *K. angustifolia* were higher in PCT than in control plots. Soil mineralizable NH_4^+-N was lower under patches of *K. angustifolia* than under patches of feather moss (*Pleurozium schreberi* spp.). Across all 24 plots, canopy openness had a positive relationship with total ericaceous shrub cover as well as with current-year rhizome length, condensed tannins and total phenolic concentrations of *K. angustifolia*.
4. Although PCT might have a positive effect on tree growth in the short-term, as foresters anticipate, our results suggest that this silvicultural treatment potentially reduces long-term site fertility and increases “growth check” of conifer seedlings following the next clearcut. Our results also suggest that the regeneration of black

spruce stands on fertile clay deposits in drier continental climates will not be as negatively impacted by PCT.

2.3 Introduction

Boreal ericaceous shrubs, such as sheep laurel (*Kalmia angustifolia* L.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), are a concern to foresters in Eastern Canada due to their competitive effects on timber crops such as black spruce (*Picea mariana* (Mill.) B.S.P.). In particular, sheep laurel (hereafter referred to as *Kalmia*) can establish itself as a dominant understory species, due to its vegetative spread through rhizomatous growth. *Kalmia* continues to spread in old-growth forests as canopy gaps appear and, under certain conditions, can dominate the early-seral shrub layer after wildfire or clearcutting (Damman, 1971; Franklin, Gillespie, Titus, & Pike, 1994). This domination of *Kalmia* and other ericaceous shrubs on disturbed forest sites may result in "growth check" of regenerating conifer seedlings (Titus, Sidhu, & Mallik, 1995). Thiffault, Titus, and Munson (2004) have shown that *Kalmia*'s interference with black spruce growth may be due to direct competition for soil resources, arising from *Kalmia*'s relatively high root biomass and root surface area. Other studies have evoked the possibility of indirect competition by ericaceous shrubs through the production of phenolic compounds (Preston, 1999). For example, Mallik (1987) found that aqueous extracts of *Kalmia* litter inhibited primary root elongation of black spruce germinants. Likewise, Yamasaki, Fyles, Egger, and Titus (1998) observed lower mycorrhizal colonization of black spruce seedlings in proximity to *Kalmia*. Both of these studies hypothesized that phenolic compounds produced by *Kalmia* may exert allelopathic effects on black spruce.

While the allelopathic potential of ericaceous shrubs remains uncertain, there is clearer evidence that ericaceous shrubs gain a competitive advantage over black spruce seedlings by producing large quantities of condensed tannins. These compounds, also referred to as proanthocyanidins, are polymers consisting of three-ring flavanols joined with C-C bonds, and are a subset of phenolic compounds. When released from leaf litter, condensed tannins

form stable complexes with soil protein, thus preventing soil organic N from mineralising to inorganic N (Joanisse, Bradley, Preston, & Bending, 2009). Joanisse, Bradley, Preston, and Munson (2007) showed that condensed tannins may comprise up to 23 % of *Kalmia* leaf litter dry mass. *Kalmia* tannins have proven to be extremely effective at reducing N mineralization in black spruce forest floors (Bradley, Titus, & Preston, 2000; Joanisse et al., 2009; Joanisse, Bradley, & Preston, 2018). *Kalmia* litter tannins have also been shown to reduce extracellular soil enzyme activity (Joanisse et al., 2007), further reducing soil nutrient cycling. However, tannin-related declines in nutrient cycling do not adversely affect ericaceous shrubs to the same extent as they do conifer seedlings. This is likely due to the shrubs' associations with ericoid mycorrhizae, which can efficiently acquire N from tannin-protein complexes (Bending & Read, 1996; Joanisse et al., 2007). Thus, the production of leaf litter tannins combined with ericoid mycorrhizal associations are two characteristics that make ericaceous shrubs highly competitive on some regenerating black spruce sites in Eastern Canada.

It is unclear why conifer growth check in the presence of ericaceous shrubs varies across different regenerating sites. There are some reports that growth check is less likely to occur on sites with naturally high soil fertility (Bradley, Fyles, & Titus, 1997). More specifically, soil nutrient mineralization rates are key determinants of black spruce competitiveness, as black spruce roots have a higher affinity for mineral nutrients than do ericaceous shrubs (Thiffault et al., 2004). This is corroborated by field trials that reported a release of conifer seedlings from growth check following mineral fertilizer applications (Bradley, Titus, Preston, & Bennett., 2000; Lebel, Thiffault, & Bradley, 2008; Moroni, Thiffault, Titus, Mante, & Makeschin, 2009). High soil fertility thus allows conifers to reach canopy closure, which in turn triggers a reduction in the growth rates of ericaceous shrubs (Huffman, Zasada, & Tappeiner, 1994a). On the other hand, low site fertility may promote the production of foliar tannins (Bryant, Chapin, & Klein, 1983), further reducing soil fertility and increasing ericaceous shrub cover. Thus, in order to sustain yields over consecutive forest rotations, it is

important that silvicultural treatments maintain a certain threshold of soil fertility during stand development.

What might strongly control soil fertility on regenerating black spruce sites is the extent to which understory ericaceous shrub communities develop, both aboveground and belowground, prior to forest disturbance. Huffman et al. (1994a) performed a shading experiment on salal (*Gaultheria shallon* Pursh) which showed that the optimal growth of above- and belowground components of this ericaceous shrub occurred at 50-70% natural sunlight. Huffman, Tappeiner, and Zasada (1994b) further showed that salal rhizome and aerial stem biomass were negatively correlated with the density of overstory trees. Thus, forest canopy gaps may increase the cover of understory ericaceous shrubs as well as the proliferation of their rhizomes. Furthermore, the carbon- nutrient balance theory as well as empirical evidence (Bryant et al., 1983; Joanisse et al., 2018) suggest that increased light conditions in canopy gaps would increase foliar tannins and decrease overall litter quality (e.g. lower specific leaf area and lower foliar N), thus exacerbating a decrease in soil N cycling. If canopy gaps were also to increase belowground rhizome growth, then this would increase the number of vegetative buds that could potentially lead to new shoots after forest harvesting.

Climate is another factor that could determine the abundance of ericaceous shrubs in forest understories and their dominance following forest disturbance. For example, *Kalmia* occurs in continental climates such as in Northern Ontario (Canada), but there is a paucity of reports of a conifer growth check problem in these regions. Instead, ericaceous shrubs in these continental climates are mainly discussed in terms of their conservation value in creating habitat for wildlife (Walker, 2001; Baycroft, 2001; Ministry of Natural Resources North Bay District, 2002). Conversely, the spread and dominance of ericaceous shrubs is a common occurrence in Canadian Maritime provinces, including large *Kalmia* heathlands formed

following the harvesting or burning of mature black spruce stands (Damman, 1971; Meades, 1983; Mallik, 1995; Thiffault, Titus, & English, 2017). This may be due to slower decomposition rates in humid climates, resulting in thick lignin-rich forest floors that favor the spread and dominance of ericaceous shrubs. For example, Huffman et al. (1994b) showed that the emergence and survival of salal was favored on moist woody substrates compared to mineral soil.

In the province of Quebec, Canada, forestry practices are said to be "extensive". In other words, forest management strives to lower operating costs by using only a few silvicultural treatments during an entire forest crop rotation. One of these treatments is pre-commercial thinning (PCT), commonly performed 15-20 years after stand establishment. PCT is the removal of non-crop trees as well as a reduction in the density of commercial species such as black spruce. The objective of PCT is to increase the growth rate of the remaining stems by lowering competition for light and soil resources, thereby shortening the rotation age of the forest (Smith, 1986). In doing so, however, PCT creates canopy gaps as well as a pulse of lignin-rich woody substrates into the forest floor. As previously discussed, these two factors may contribute to the spread of *Kalmia* and other ericaceous shrubs in the understory, to an increase in tannin production and to lower N cycling. In other words, we hypothesized that PCT predisposes a site to conifer seedling growth check once the stand has matured and is ready for harvesting. We further hypothesized that PCT would stimulate the spread of ericaceous shrubs in the understory more so on nutrient-poor than on nutrient-rich sites, and more so in a humid than in a dry climate regime. We therefore conducted a study where we measured the above and below ground spread of ericaceous shrubs, their foliar and rhizome traits, as well as soil N mineralization rates in mid-rotation black spruce stands previously treated to PCT and in adjacent untreated control stands. Plots were selected to test for interactions between PCT and soil fertility, and between PCT and climate regime.

2.4 Materials and Methods

Field sites and experimental design

The study was conducted in 12 boreal forest sites in the province of Quebec, Canada. Four sampling sites were established 150 km north of the town of Baie-Comeau within the Lake Cacaoui ecological region (ca. 50° N 68° W), located in the spruce-feather moss bioclimatic domain (Morneau & Landry, 2010). These will be referred to as the Côte-Nord sites which is the name of the region the sites are located within (Fig. 2.1). Soils in the region have developed on glacial till geological deposits. Mean annual temperature is -1.0 °C with a growing season of ca. 140 days. Mean annual precipitation over the region is 1100–1300 mm, 35% to 40% of which falls as snow (Morneau & Landry, 2010). The remaining eight sampling sites were established in the Abitibi region (ca. 49° N, 78° W), within the balsam fir–yellow birch bioclimatic domain (Blouin & Berger, 2002). Four of these sites were located on glacial till geological deposits (Gosselin, 2003) and will be referred to as the Abitibi till sites. The other four sites were located on fine-textured glacio-lacustrine clay deposits (Blouin & Berger, 2002) and will be referred to as the Abitibi clay sites. Mean annual temperature is 2.5 °C with a growing season of ca. 150 to 160 days. Mean annual precipitation is 800–900 mm, 30% of which falls as snow (Blouin & Berger, 2002). Thus our experimental design comprised of replicated (n=4) paired plots (PCT vs control) in each of three site types (Côte-Nord, Abitibi till and Abitibi clay).

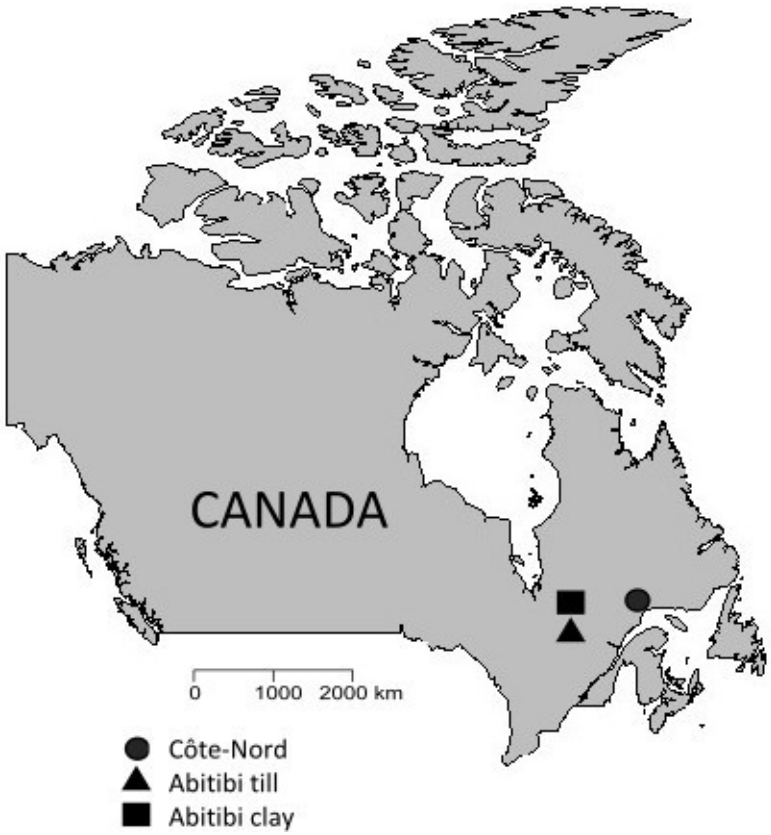


Figure 2.1 Location of PCT sites in the regions of Abitibi and Côte-Nord, Quebec, Canada on till or clay soil deposits. At the time of thinning, sites were randomly established between 1995 and 1999.

The 12 sites were selected based on several criteria including tree species composition, stand age, date of PCT treatment, drainage, topography and slope, using the database known as "*Réseaux des placettes-échantillons permanentes du Québec meridional*", which was provided by Quebec's Ministry of Forests, Fauna and Parks (MFFP). Stands were dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) with balsam fir (*Abies balsamea* (L.) Mill.) occasionally occurring in small amounts (i.e. < 20% overstory cover). The understory ericaceous shrub layer was dominated by sheep laurel (*Kalmia angustifolia* L.), Labrador tea

(*Rhododendron groenlandicum* (Oeder) Kron & Judd) and various blueberry species (*Vaccinium* spp.). The remaining understory vegetation was mainly comprised of speckled alder (*Alnus rugosa* (Du Roi) R.T. Clausen) and leatherleaf (*Chamaedaphne calyculata* (L.) Moench). The ground cover was dominated by red stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.), with occasional peat moss (*Sphagnum* L.) on the wettest sites and occasional reindeer lichen (*Cladonia* spp.) on the driest sites. The Côte-Nord and Abitibi till sites were moderately to well drained whereas the Abitibi clay sites were imperfectly drained due to the fine textured clay (Blouin & Berger, 2002; Gosselin, 2003; Morneau & Landry, 2010). All sites had been harvested between 1974-1982 and part of the clearcut area had been PCT treated between 1995-1999. The PCT treatment was randomly applied with respect to relevant environmental conditions. The same year PCT treatments had been applied, an 11 m radius plot was randomly established by MFFP technicians within the PCT treated area as well as within the adjacent non-treated area (i.e. control plot). The distance between treated and control plots on each site varied between 100-300 m.

Field sampling

In mid-July 2016, two 22 m transects were established perpendicular to each other within treated and control plots at each site. Six sampling points were established at 2, 5, 8, 14, 17 and 20 m along each transect. In mid-July 2016, a hemispheric photo of the canopy was taken at each sampling point using a Nikon fisheye converter FC-E8 0.21x lens attached to a Nikon Coolpix 5000 camera set at 1 m height.

In mid-July 2016, the percent ground cover of understory shrubs was visually assessed in each of the 24 plots. More specifically, a visual estimation of percent ground cover was taken by the same observer within a 1 m radius circle surrounding each sampling point, along the

two perpendicular transects used to sample canopy openness. The visual estimate of percent ground cover from each sampling point was averaged together for a mean percent ground cover of the plot.

In mid-July 2016, a 5 L sample of forest floor F-layer material (Soil Classification Working Group, 1998) was collected at each sampling point in each plot, and sieved on site through 5 mm wire mesh. F-layer material was taken because this is the layer N is preferentially acquired by ericaceous shrubs and black spruce. Samples were transferred into sealed plastic bags, placed under ice packs in coolers, transported to the laboratory (U. Sherbrooke) and stored at 4 °C until analyzed. In mid-July 2017, a forest floor F-layer sample (ca. 5 L) was taken under each of three *Kalmia* patches and three *Pleurozium* patches in each plot. The three *Kalmia* and three *Pleurozium* patches in each plot were at least 10 m apart from each other. These were sieved and transported to the laboratory in the same way as forest floor samples collected the previous year.

Current and second year *Kalmia* and Labrador tea leaves were collected separately at each of the 12 sampling points in each plot, except when they were absent. These were transported to the laboratory in coolers and stored at 4 °C until analyzed. Also in 2016, eight 1 m^2 litter traps were placed under both *Kalmia* and Labrador tea patches, in each of the 24 plots. *Kalmia* and Labrador tea leaf litters were collected from each litter trap in mid-July 2017, sorted by species and transported in paper bags to the laboratory and stored at 4 °C. In mid-July 2017, current-year *Kalmia* rhizomes were collected in each plot. These were identified by their characteristic pink-white flesh and apical meristem. We first manually removed the moss or lichen cover by hand down to the forest floor, near *Kalmia* patches. A hand cultivator rake was then used to carefully scrape through the forest floor until current-year rhizomes were found. These were verified as belonging to *Kalmia* by following the older suberized portion of the rhizome back to the source shrub. Given our sampling schedule, we

were able to collect between 20-40 rhizomes in each plot. The length of current-year rhizome growth and the total number of vegetative buds along this length were measured in the field. These were then transported to the laboratory in coolers and stored at 4 °C until analyzed.

Laboratory analyses

Canopy openness at each sampling point was estimated by analyzing canopy photos with the Gap Light Analyser (Version 2.0) software (Frazer, Canham, & Lertzman, 1999).

Mineralizable N in each of the 2016 and 2017 forest floor samples was measured using aerobic incubations. Duplicate 5 g (dry wt. equiv.) subsamples were transferred into mason jars, covered with a polyethylene film and left to incubate for 30 days at room temperature. These were then extracted in 50 mL of 1 M KCl aqueous solution, filtered through Fisherbrand™ P5 filter paper and analyzed colorimetrically for NH_4^+-N (salicylate–nitroprusside-hypochlorite) using an Astoria 2 Analyzer (Astoria Pacific Inc., Clackamas, OR).

For each plot, we measured the surface area of 100 second-year *Kalmia* and Labrador tea leaves using the program WinFOLIA – V.2001a (Regent Instruments Inc., Quebec, Canada). Leaves were then freeze-dried and weighed in order to calculate specific leaf area (SLA). Specific rhizome mass (SRM) in each plot was calculated by dividing the total oven dry (65 °C) mass of rhizomes by total rhizome length.

The remaining current and second-year *Kalmia* and Labrador tea leaves, and the *Kalmia* and Labrador tea litters, were freeze-dried whereas the 2016 forest floor samples were oven-dried (65 °C). Samples were ground to a fine powder using a Retsch model MM200 ball mill (Retsch GmbH & Co., Haan, Germany). An 80–100 mg ground subsample was encapsulated in Sn and analyzed for total C and N by high temperature combustion and thermo-conductometric detection, using a Vario Macro dry combustion analyzer (Elementar Analysensyteme GmbH, Hanau, Germany). Foliar % N resorption was used as an index of N use efficiency using the following equation (Chapin & Kedrowski, 1983):

$$\text{Foliar \% N resorption} = \frac{[Nitrogen]_{second-year} - [Nitrogen]_{litter}}{[Nitrogen]_{second-year}} \times 100\%$$

Equation 2.1 Foliar % N resorption equation as an index of N use efficiency.

A 10-15 mg aliquot of each ground *Kalmia* leaf and litter subsample was extracted with 10 mL of acetone:water (70:30) and analyzed for total extractable phenolics by the Folin-Ciocalteu assay, and for condensed tannins by the butanol-HCl assay (Waterman & Mole 1994; Preston, Trofymow, Sayer, & Niu, 1997). Total phenolics were standardized against tannic acid (Fisher Scientific) whereas tannins were standardized against purified *Kalmia* condensed tannins (Preston, 1999).

Statistical analyses

We used mixed model two-way ANOVAs to test the effects and possible interactions of treatment (i.e. PCT vs control) and site type, on each of the response variables. When it was warranted, we also tested for specific interactions between treatment and soil deposit (i.e.

Abitibi till vs. Abitibi clay) or between treatment and climate regime (i.e. Côte-Nord vs. Abitibi till). Our models were run using the function *lmer* of the package *lme4* in R statistical software v.3.4.2 (Bates, Mächler, Bolker, & Walker, 2015; R Core Team, 2017). The site intercept was the random effect variable and the R code used was Y~ X + site-type + (1|site). When significant interactions were found, one-way mixed model ANOVAs were used to test the effect of treatment within each individual site-type, with the identity of each site used as a random effects variable. When significant effects were found, a post-hoc Tukey's HSD test was performed for comparing means.

Multiple linear regression analysis was used to test the relationship between canopy openness and selected response variables, using the function *lm* of the package *stats* in R software v.3.4.2 (R Core Team, 2017). We included site-type as a fixed effect variable in our models because the range of canopy openness values varied between site-types.

Prior to analyses, all data were verified for normality and homogeneity of variance assumptions, and the level of significance for all tests was set to $P \leq 0.05$, unless otherwise reported.

2.5 Results

PCT effects on canopy openness and ericaceous shrub cover

PCT plots had significantly greater canopy openness than control plots in Abitibi clay (25.8 % vs. 20.5 %, $P < 0.001$) and Abitibi till (16.5 % vs. 14.5 %, $P = 0.003$) sites. In Côte-Nord,

mean canopy openness was likewise higher in PCT than in control plots (22.3 % and 20.5 %), but that difference was not statistically significant. The range of canopy openness values were 13.2 % to 37.1 % in Abitibi clay, 13.2 % - 22.4 % in Abitibi till, and 18.4 % - 26.6 % in Côte-Nord sites.

Kalmia cover was significantly (P = 0.015) higher in Côte-Nord (16.0 %) than in both Abitibi till (5.1 %) and Abitibi clay (2.9 %) sites (Fig. 2.2A). Labrador tea cover was significantly (P = 0.016) higher in Côte-Nord (19.4 %) than in Abitibi till (0.7 %) sites (Fig. 2.2B). Across all three site-types, the cover of *Vaccinium* spp. was significantly (P = 0.026) higher in PCT (9.5 %) than in control plots (3.4 %) (Fig. 2.2C), as was the total cover of all ericaceous shrubs (31.6 % on PCT, 19.2 % on control) (P = 0.004; Fig. 2.2D). Total ericaceous shrub cover was significantly (P = 0.017) higher in Côte-Nord (43.9 %) than in Abitibi till (12.1 %) sites (Fig. 2.2D). Neither PCT treatment nor site-type had a significant effect on leatherleaf cover.

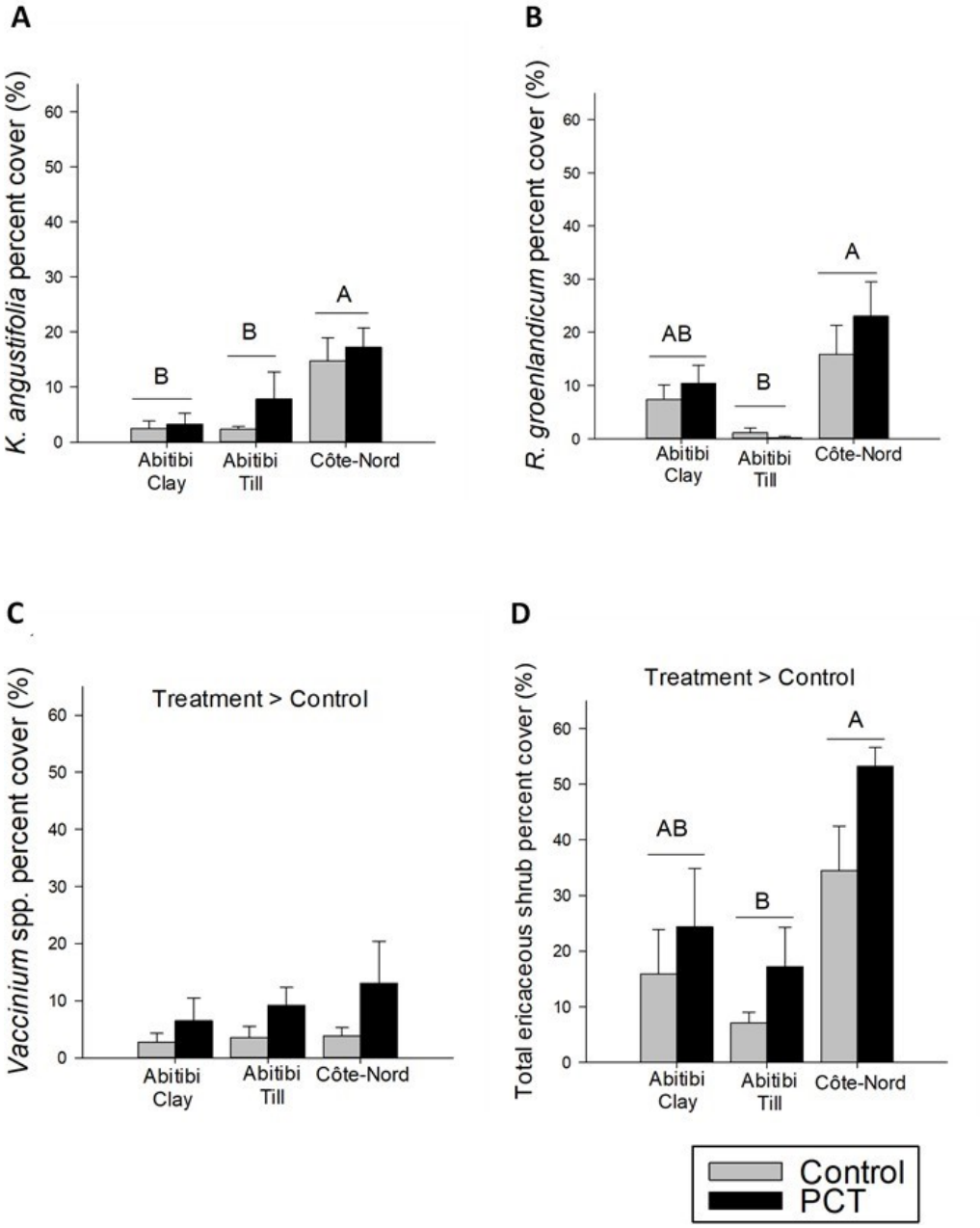


Figure 2.2 **Average ericaceous shrub cover on PCT (black bars) and control plots (grey bars) across site types. The four panels report the average cover of *K. angustifolia* (A), *R. groenlandicum* (B), *Vaccinium* spp. (C) and total ericaceous shrubs (D). Different upper-case letters indicate significant differences between site types. Significant main effects of treatment are indicated at the top of the frame. Vertical lines = 1 S.E.**

There was a significant (P = 0.008) interaction between PCT and site type controlling current annual rhizome length (Fig. 2.3A). More specifically, PCT plots had significantly longer current annual rhizomes in the Abitibi till (8.3 cm) (P < 0.001) and Côte-Nord (7.2 cm) (P < 0.001) sites compared to control plots (6.3 cm and 5.8 cm respectively), but not in the Abitibi clay sites (6.5 cm on PCT plots and 6.1 cm on control plots). Although the interaction between PCT and site type on SRM fell below our threshold of statistical significance (P = 0.103), we nevertheless found significantly higher SRM in PCT than in control plots in Abitibi till (4.2 mg cm^{-1}) (P = 0.005) and Côte-Nord (3.8 mg cm^{-1}) (P = 0.011) sites compared to control plots (2.4 mg cm^{-1} and 3.3 mg cm^{-1} respectively), but not in Abitibi clay sites (3.5 mg cm^{-1} on PCT plot and 3.3 mg cm^{-1} on control plots) (Fig. 2.3B).

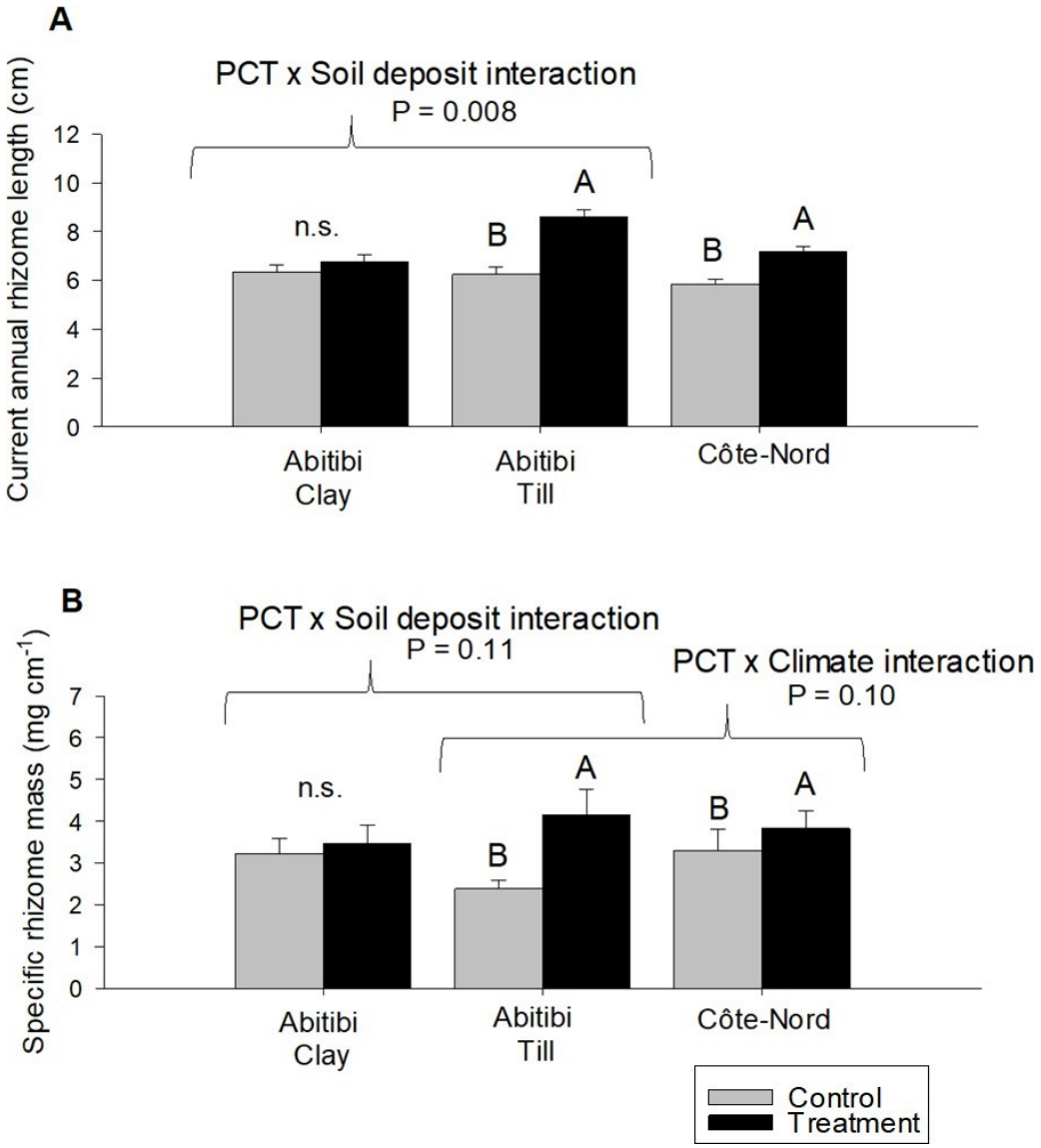


Figure 2.3 **Average current annual rhizome length (A) and specific rhizome mass (B) on PCT (black bars) and control plots (grey bars) across site types. Horizontal brackets report the significance level of PCT x Deposit or PCT x climate interactions. Different upper-case letters indicate significant differences between treatments within a given site type. Vertical lines = 1 S.E.**

Across all sites, there was a significant positive relationship ($R^2 = 0.74$, $P < 0.001$) between canopy openness and total ericaceous shrub cover (Fig. 2.4), when controlling for the effect of site-type.

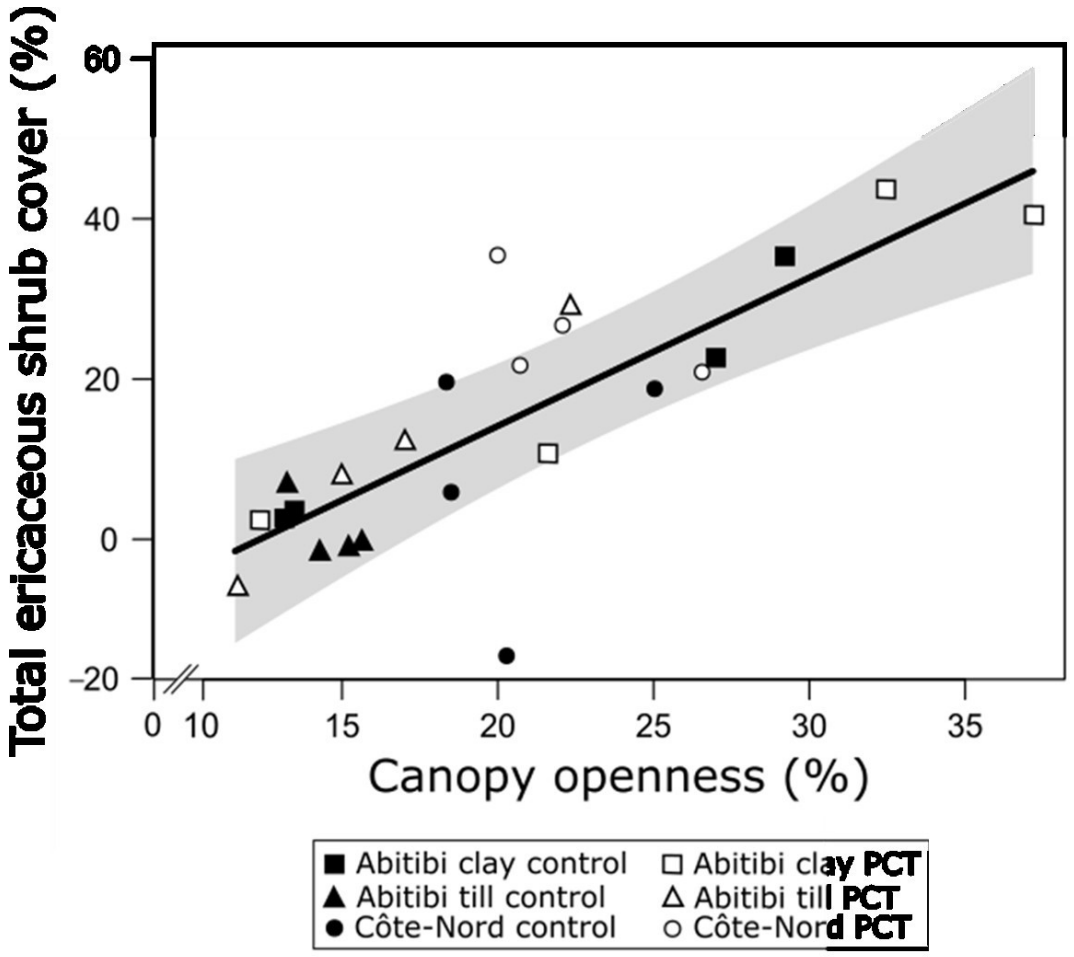


Figure 2.4 **Significant ($P < 0.001$) relationship between canopy openness and total ericaceous shrub cover, based on multiple linear regression analysis. The plot includes the expected values (regression line), the 95% confidence interval for the expected values, and partial residual values after controlling for site type (symbols).**

Likewise, there was a significant positive relationship ($R^2 = 0.28$, $P = 0.010$) between canopy openness and current annual rhizome length of *Kalmia* (Fig. 2.5), when controlling for the effect of site-type.

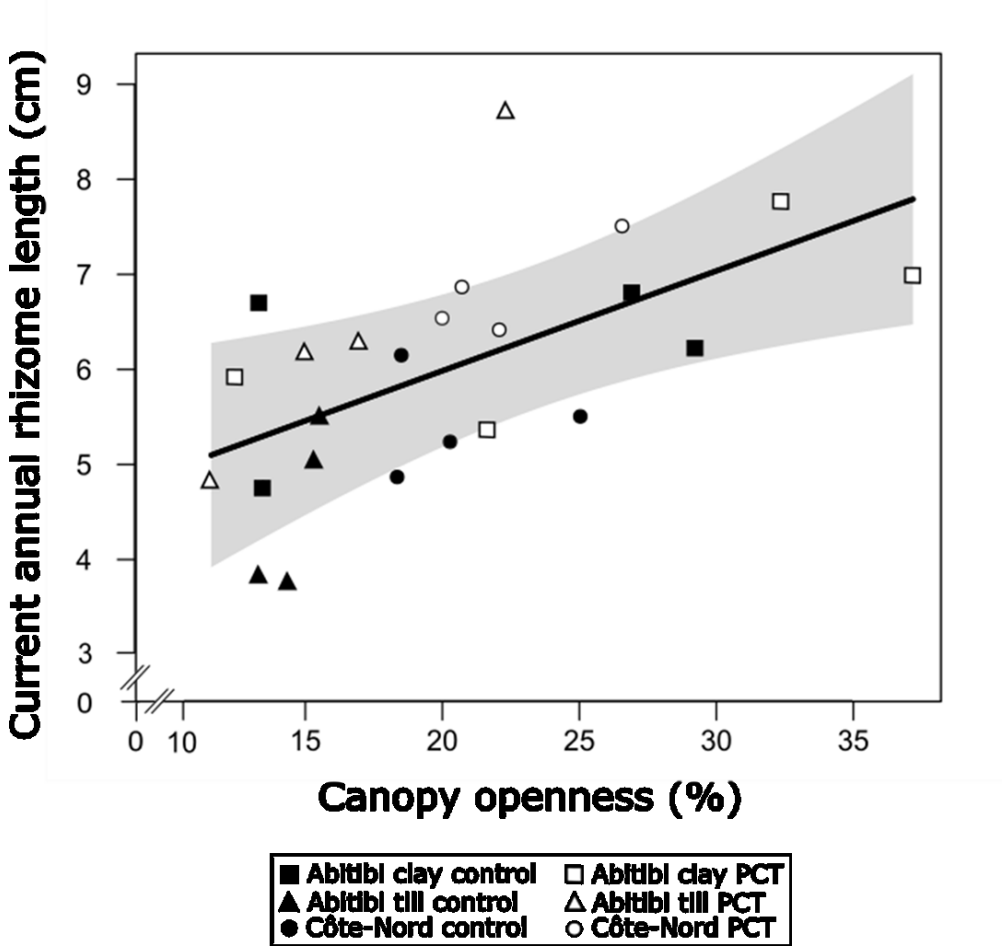


Figure 2.5 **Significant ($P < 0.010$) relationship between canopy openness and current annual rhizome length, based on multiple linear regression analysis. The plot includes the expected values (regression line), the 95% confidence interval for the expected values, and partial residual values after controlling for site type (symbols).**

Forest floor properties

Average forest floor depth was significantly (P = 0.020) higher in Côte-Nord (16.1 cm) than in Abitibi clay (7.8 cm) sites. Neither PCT nor site-type had a significant effect on mineralizable N in forest floor samples collected in 2016, which are total plot averages. However, forest floor samples collected in 2017 revealed a significant (P = 0.037) interaction between vegetation patch type (i.e. *Pleurozium* vs. *Kalmia*) and site type (Fig. 2.6). More specifically, mineralizable N was lower under *Kalmia* than under *Pleurozium* patches in both Côte-Nord (3.9 µg g^{-1} and 11.1 µg g^{-1} respectively) (P = 0.042) and Abitibi till (13.9 µg g^{-1} and 50.2 µg g^{-1} respectively) (P = 0.063), but not in Abitibi clay (35.9 µg g^{-1} and 24.3 µg g^{-1} respectively).

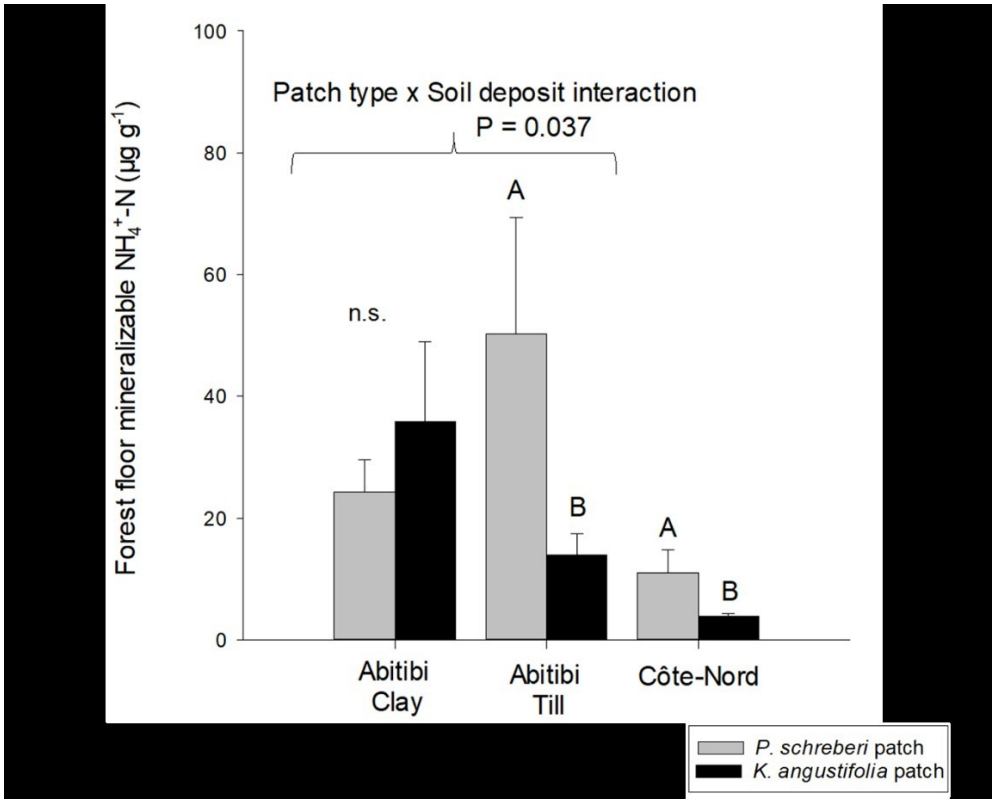
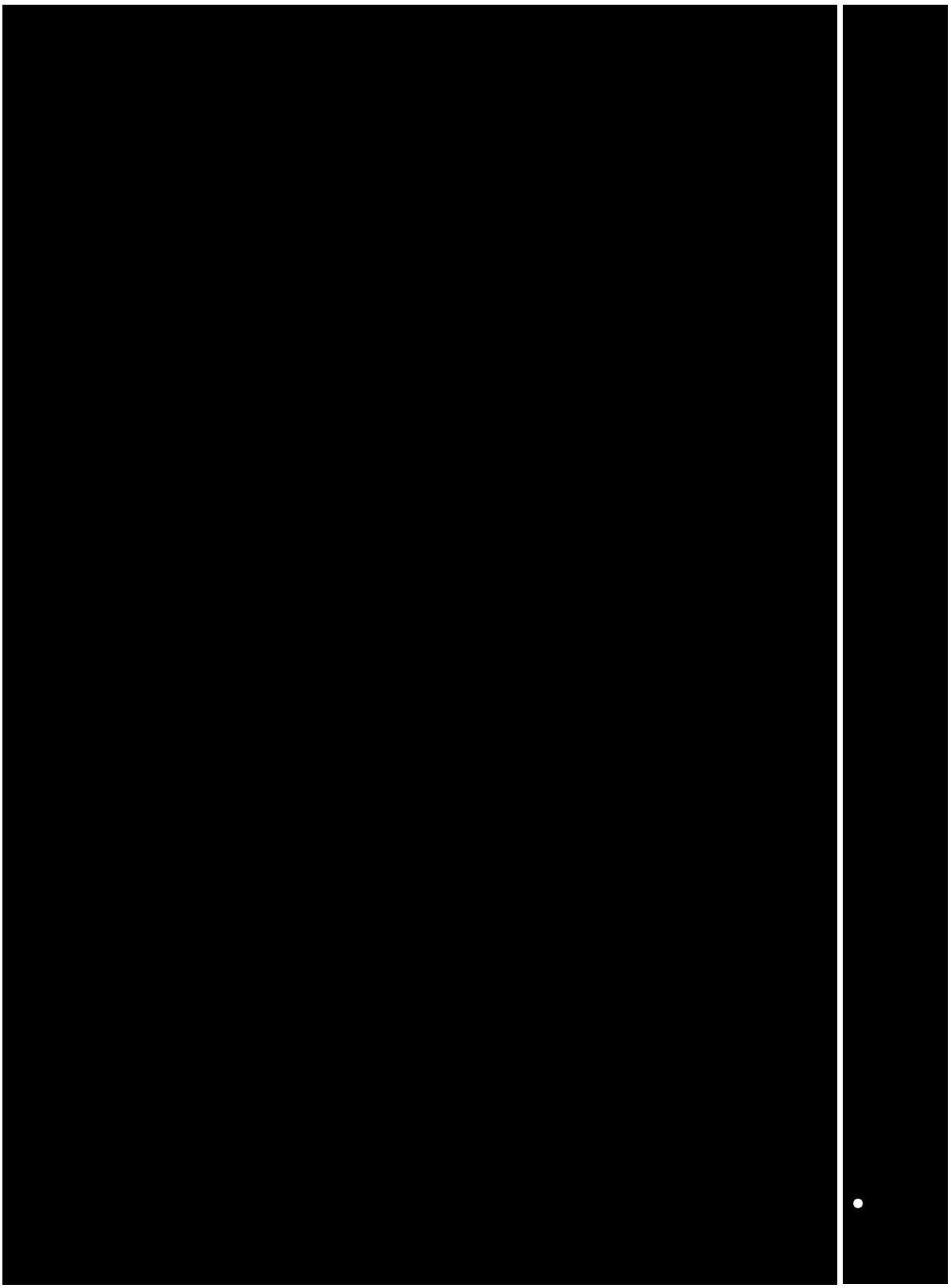


Figure 2.6 **Forest floor mineralizable N under *K. angustifolia* and *P. schreberi* patches in each site type. Different upper case letters indicate differences between patch type within Côte-Nord (P = 0.042) and Abitibi till (P = 0.063) sites. Horizontal bracket reports the significance level of the PCT x soil deposit interaction. Verticals lines = 1 S.E.**

Kalmia *and Labrador tea foliar properties*

The foliar N concentration of current *Kalmia* leaves was significantly ($P < 0.001$) higher, whereas as the C:N ratio was significantly ($P < 0.001$) lower, in Côte-Nord than in both

Abitibi till and Abitibi clay sites (Table 2.1). The C:N ratio of current *Kalmia* leaves was also significantly (P = 0.049) higher in PCT than in control plots across all sites. SLA of second-year *Kalmia* leaves was significantly (P = 0.014) higher in Abitibi till than in Cote-Nord sites. *Kalmia* litter N concentration was significantly higher (P = 0.002), whereas the C:N ratio was significantly (P = 0.002) lower, in Abitibi till than in Côte-Nord. *Kalmia* % N resorption was significantly (P = 0.002) higher in Côte-Nord than in Abitibi till and Abitibi clay. As for Labrador tea, condensed tannins, total phenolics and the C:N ratio of current leaves were significantly (P = 0.030, 0.032 and 0.035 respectively) higher in Abitibi clay than in Côte-Nord, whereas the opposite pattern was observed for foliar N (P = 0.013). The condensed tannin concentration of Labrador tea leaf litter was significantly (P = 0.036) higher in Abitibi clay than in Cote-Nord sites. Labrador tea % N resorption was significantly (P = 0.022) higher in Côte-Nord than in Abitibi clay.



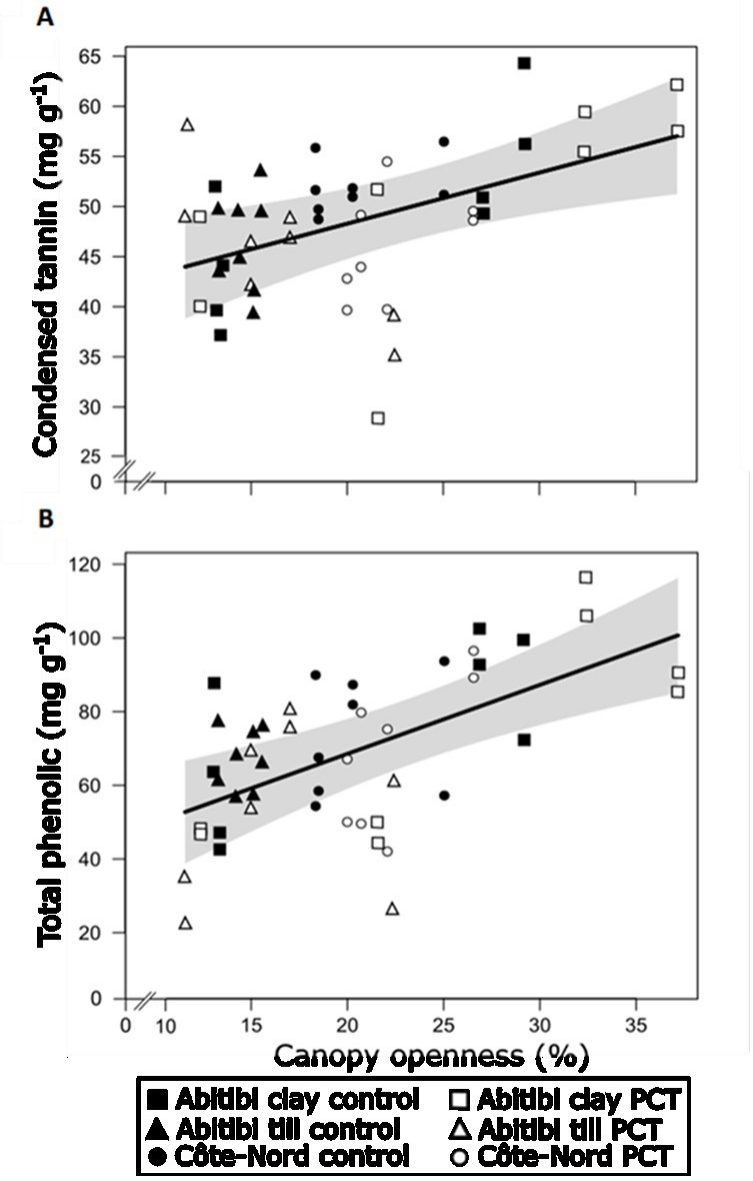


Figure 2.7 **Significant (P = 0.004 and P < 0.001) relationships between canopy openness and condensed tannins (A), and between canopy openness and total phenolic concentrations (B) of *Kalmia* leaves (current and 2-y-old), based on multiple linear regression analysis. The plots include the expected values (regression lines), the 95% confidence intervals for the expected values, and partial residual values after controlling for site type (symbols).**

Across all sites, there were significant positive relationships between canopy openness and *Kalmia* condensed tannins ($R^2 = 0.18$, $P = 0.004$) as well as *Kalmia* total phenolics ($R^2 = 0.24$, $P < 0.001$), when controlling for the effect of site-type (Fig. 2.7A, B).

2.6 Discussion

Growth response of ericaceous shrubs to PCT

Our study confirmed that PCT generally increased the cover of ericaceous shrubs in the understory of black spruce stands, approximately 20 years after treatment. This is in support of a study conducted in southern Vancouver Island that observed an increase of salal after forest thinning (He and Barclay, 2000). Although this effect was not consistently significant, the trend was consistent for all species with the exception of Labrador tea on Abitibi till sites, where the average cover of this species was very low (< 1%). We note with interest, the lack of PCT x soil deposit and PCT x climate interactions controlling ericaceous shrub cover. While this contradicts our predictions, the observed general trend across all site types suggests that a positive effect of PCT on the spread of ericaceous shrubs can be generalized over a large portion of Quebec's boreal black spruce domain.

Ericaceous shrub cover was higher in Côte-Nord than in Abitibi till sites, in accordance with our prediction that maritime climates are more conducive to the spread of ericaceous shrubs than drier climates. Litter decomposition rates are typically slower in maritime climates, leading to thicker forest floors. This may in turn improve the competitive ability of

ericaceous shrubs because of their association with ericoid mycorrhizae, which are adapted to acquire organic forms of soil nutrients (Read, 1996; Joanisse et al., 2009). This is corroborated by Mallik and Kravchenko (2018) who found a positive relationship between forest floor thickness and *Kalmia* cover in Newfoundland. It should be concerning to foresters that total ericaceous shrub cover on the dryer Abitibi till sites nevertheless increased to 18% due to PCT. This amount of *Kalmia* cover was shown to significantly reduce black spruce seedling growth after forest disturbance in the Abitibi till region (Lebel et al., 2008).

Although *Kalmia* produces flowers that ripen into small dehiscent capsules bearing abundant short-lived seeds, the reproduction and spread of this shrub remains primarily vegetative (Van Deelen, 1991). *Kalmia* is a clonal species that expands laterally as aerial sprouts emerge from dormant buds on rhizomes. Hence, the three belowground traits that we measured all related to the effect of PCT on the *Kalmia* bud bank. While PCT had no effect on the number of buds per rhizome length, we did observe an increase in the mean annual growth of rhizomes as well as in the specific rhizome mass (SRM) on the Abitibi till and Côte-Nord sites. SRM is the reciprocal of specific rhizome length (SRL), often used in root ecology (i.e. specific root length) as an index of a plant's benefit relative to its cost of producing roots. This is a logical conjecture for roots, whose primary purpose is to acquire soil resources. However, the primary role of *Kalmia* rhizomes is not to acquire soil resources, but to produce new stems. Hence, SRM is the proper benefit-to-cost index for rhizomes as it reflects the carbon reserve available for vegetative buds to sprout into shoots. Thus, PCT on the Abitibi till and Côte-Nord sites not only increased *Kalmia*'s bud bank by increasing mean annual growth of rhizomes, but it also produced more vigorous buds by increasing SRM.

The lack of a PCT effect on rhizomes at the Abitibi clay sites (i.e. PCT x soil deposit interaction) suggests that high soil fertility could mitigate the presumptive stimulatory effects of higher light availability or woody debris on *Kalmia* rhizome growth. It is worth

mentioning that PCT also had little effect on aboveground *Kalmia* cover on the same Abitibi clay sites, in comparison to *Rhododendron* or *Vaccinium*. Our decision to sample only *Kalmia* rhizomes was based on a time-constraint to perform the fieldwork and on the fact that *Kalmia* is the most studied species in terms of its interference with conifer seedling growth. Clearly, more research is required to better understand how soil fertility interacts with environmental factors in controlling the belowground bud bank of other ericaceous shrub species.

Foliar, litter and forest floor properties

Ericaceous shrubs respond to different light conditions by adjusting physiological and morphological properties of their leaves (e.g. Hebert, Thiffault, Ruel, & Munson 2010; Mallik, Wang, Siegwart-Collier, & Roberts, 2012). For example, low canopy openness should result in a high SLA as a means of increasing photosynthetic capacity under limited light conditions. Likewise, low light environments should decrease nutrient-to-carbon limitations. This, in turn, should result in higher foliar N, lower foliar C:N ratio, and a lower production of C-based secondary metabolites such as phenolics (Bryant et al., 1983). For these reasons, we expected control plots to display higher SLA and N concentrations, and lower C:N ratios and phenolic concentrations, than PCT plots. This is consistent with most of the *Kalmia* foliar and litter data reported in Table 1, even though most of these comparisons were non-significant. On the other hand, foliar and litter characteristics of Labrador tea were quirky, sometimes in agreement (e.g. total phenolics in Abitibi Clay), while sometimes in contradiction (e.g. condensed tannins in Côte-Nord) with expectations. The overall lack of significant PCT effects on foliar and litter properties of both species might be due to the small differences in canopy openness between PCT and control plots within each site (2-5 %). At the time PCT treatments were applied, approximately 20 years earlier, the differences

in canopy openness between treated and control plots were likely to have been greater, and differences in *Kalmia* foliar properties could have been more distinct.

The chemical quality of *Kalmia* litter may reduce enzyme activities and rates of N mineralization in forest floors (Joanisse et al., 2007; Joanisse et al., 2009). Thus, we expected the spread of *Kalmia* and other ericaceous shrubs in PCT plots would increase ericaceous shrub litter and decrease N mineralization rates across the whole plot. As canopy gaps are expected to decrease SLA and foliar N concentrations, and to increase C:N ratios and phenolic concentrations, this should further exacerbate the negative effect of PCT on N mineralization rates. The fact that we did not detect significant differences in the mean N mineralization rates of PCT and control plots in 2016 suggests that *Kalmia* cover was still insufficient to adversely affect N cycling across the whole plot. However, since N mineralization rates under *Kalmia* patches were significantly lower than under *Pleurozium* patches on two of the three site types, in 2017, is cause for concern to foresters. We can expect *Kalmia* on these sites will spread further in the understory as trees die off and canopy gaps appear. The fact that N mineralization under *Kalmia* patches in Abitibi clay did not differ than under *Pleurozium* patches demonstrates the importance of geologic parent material in determining the relative impacts of ericaceous shrubs on soil nutrient cycling. Clay sites in the Abitibi region generally have a higher pH, higher CEC (cation exchange capacity) and higher base cation concentrations compared to till soils (Bauhus, Pare, & Cote, 1998; Lamarche, Bradley, Paré, Légaré, & Bergeron, 2004). This favors the complexing of tannins with metal cations, as opposed to tannins forming hydrogen bonds with proteins and reducing N cycling (Goldstein & Swain, 1965; Haslam, 1988; Kawamoto, Nakatsubo, & Murakami, 1996; Kawamoto, & Nakatsubo, 1997).

There were significant differences in *Kalmia* foliar and litter properties between Abitibi till and Côte-Nord sites. These site type effects are more difficult to interpret as they may be due

to differences in climate regimes, plant phenology, sampling dates, regional genotypes, soil fertility or canopy openness. For example, the average SLA of second year *Kalmia* leaves was higher in Abitibi till than in Côte-Nord, consistent with the lower canopy openness in Abitibi till sites (13 – 22 %) compared to Côte-Nord (18 – 27 %). On the other hand, the higher foliar N and lower C:N ratio of current year *Kalmia* leaves in Côte-Nord might be interpreted as there being a higher soil N fertility than in Abitibi till. However, nutrient concentrations of current year leaves are notoriously variable and unreliable for diagnostic assessments of soil fertility (Linder, 1995). The fact that *Kalmia* N-use efficiency was higher in Côte-Nord, as reflected by a lower litter N, a higher litter C:N ratio and higher % N resorption, suggests that soil N fertility was actually lower in Côte-Nord than in Abitibi till. Efficient resorption of nutrients prior to litterfall allows the plant to conserve more N on infertile soils by re-allocating more N to current year leaves (Boerner, 1984; Yuan & Chen, 2015). As for Labrador tea, differences in foliar and litter properties were found mainly between Côte-Nord and Abitibi clay sites. Contrary to expectations, foliar and litter chemistry suggested higher soil fertility (i.e. lower tannins, phenolics and C:N, and higher N) in Côte-Nord than in Abitibi clay. However, these differences might also reflect higher average canopy openness in Abitibi clay (13 % - 37 %) than in Côte-Nord (18 % - 26 %). The fact that N use efficiency by Labrador tea was higher in Côte-Nord is in keeping with our presumption that Abitibi clay sites are more fertile.

Canopy openness may drive the competitive ability of ericaceous shrubs

Our study was mainly concerned with the effects of PCT on the response of ericaceous shrubs, and how this response varies with climate regime and soil fertility. As previously discussed, PCT may affect ericaceous shrubs in several ways including higher light availability, more woody substrates in the forest floor and lower competition for soil resources. While we do not have the data to test the effects of all of these factors

individually, it is possible to infer the importance of light availability in general. The effects of PCT on individual response variables were sometimes insignificant, presumably because differences in canopy openness between PCT and control plots within each site was relatively small (2-5 %). However, by pooling data and controlling for site type using multiple linear regression, it was possible to assess the response of ericaceous shrubs over a broad range (13 % - 37 %) of canopy openness. Data shown in figures 3, 4 and 6 strongly suggest that light availability is a major driver of above and belowground ericaceous growth in the understory, as well as leaf tannin and phenolic concentrations. This is in keeping with the notion that ericaceous shrubs gain in competitive ability as boreal black spruce forests mature, as trees die off and as canopy gaps appear. Additionally, with fewer trees, there would be an increase in resources for ericaceous shrubs to grow. In the absence of disturbance, the "climax" state of these forests (i.e. when the composition and structure does not change significantly over long time periods) is most likely to be ericaceous-dominated open spruce woodlands or, in extreme cases, heathlands (Mallik, 2003; Royo & Carson, 2006).

Forest management implications

Forestry is one of the largest economic sectors in Quebec and generates a large trade surplus for the province. Since 2005, the province has appointed an independent "Chief Forester" whose duty is to calculate the annual allowable cut (AAC) that will ensure sustainable yields into the future. This AAC is determined using simulation models that are calibrated from empirical data such as growth and yield curves from across Quebec. These curves are adjusted for specific ecological factors that define the quality of a given site. Over recent years, the phenomenon of conifer growth check induced by the invasion of ericaceous shrubs on forest cutovers has been acknowledged by the Chief Forester. In their simulations, forest

rotation age on ericaceous dominated sites is delayed by up to 25 years if not treated with proper silvicultural treatments (Bureau du forestier en chef, 2013).

Over recent decades, foresters have developed silvicultural treatments that mitigate *Kalmia*-induced conifer growth check, notably mechanical scarification and mineral N fertilization (Thiffault, Titus, & Munson, 2005; Thiffault et al., 2017). While knowing how to treat the problem may be laudable, knowing how to prevent it may be more useful, moving forward. The success of extensive forest management is predicated on an understanding of the ecological factors and life history traits that drive the competitive abilities of key plant species. We have anecdotal evidence that many foresters and ecologists in Quebec may not fully realize the niche space occupied by boreal ericaceous shrubs. When discussing the autecology of these shrubs at various forums, many participants are under the belief that these shrubs are "pioneer species" that appear following major forest disturbance such as wildfire or clearcutting. This belief is framed within a generally held model of forest secondary succession that separates early seral "pioneer" species from late-seral "old-growth" species. Typically, pioneer species are fast-growing, shade intolerant plants that are inefficient in their nutrient use (e.g. *Epilobium angustifolium* L.) whereas the opposite applies to dominant old-growth species, such as black spruce. However, *Kalmia* and similar ericaceous shrubs do not display functional traits that are consistent with typical pioneer species. For example, they produce relatively small leaves with thick cuticles, their litter is recalcitrant to decomposition, they tolerate low soil pH and shading, they successfully colonize thick forest floors, they are adept at acquiring nutrients in organic forms and they display a high longevity of the established phase. Many of these are traits are consistent with the life history strategies of stress tolerators (Grime, 1977). Thus it is essential that foresters acknowledge that boreal ericaceous shrubs establish themselves under forest canopies and that their conspicuousness following disturbance is simply a continuation of their presence on the site. In other words, boreal ericaceous shrubs should neither be dubbed as pioneer nor as old-growth species, as their life cycle straddles forest disturbance.

In order to treat the cause as opposed to the symptom of conifer growth check, it is essential that foresters understand the potential impacts of PCT on the spread and competitive ability of ericaceous shrubs. We have shown that canopy gaps created by PCT will increase the aerial cover and litter inputs, the production of phenolic substances, and the belowground budbank of ericaceous shrubs. This, in turn, predisposes a site to a higher risk of conifer growth check many years later, following timber harvest. We recommend that future research focus on the occurrence and severity of conifer growth check on clearcut sites that were previously treated with PCT. This will be useful in establishing threshold levels of canopy openness that can be tolerated in regenerating stands without compromising site fertility, as well as understanding the risks associated to PCT on different site-types.

2.7 Authors' contributions

RLB and KR conceived the ideas and all authors contributed to the designed methodology. KR collected and analysed the data and all authors contributed to the interpretation of the data. KR and RLB led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

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CHAPTER 3

SCARIFICATION SUCCESSFULLY REDUCES THE LONG-TERM COMPETITIVE ABILITY OF BOREAL ERICACEOUS SHRUBS

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3.1 Foreword

Chapter 3 focuses on the interaction between scarification and climate regime in controlling the long-term competitive ability of boreal ericaceous shrubs. Several short and long-term studies on scarification have only brought attention to conifer growth, thus, our study is one of the first to examine the response of ericaceous shrubs to long-term scarification. Additionally, our study brings further knowledge on how ericaceous shrub rhizomes respond to changes in light availability and to the mixing of the soil from the scarification process. Our study will inform forest management on the benefits of scarification at reducing the encroachment and competitive ability of ericaceous shrub. Additionally, our study will aide in the suggestion of creating specific scarification protocols based on climate regimes. The co-authors of this article are Krista Reicis, Robert L. Bradley, Gilles Joanisse, Nelson Thiffault, and Amy Wotherspoon. Robert L. Bradley and Krista Reicis conceived the ideas of the project while all co-authors aided in the design and methodology. Krista Reicis and Amy Wotherspoon collected the field samples and analyzed the data in the laboratory with the aid of Gilles Joanisse. Krista Reicis performed the statistics on the data and all co-authors contributed to the interpretation of the data. Krista Reicis led the writing of the manuscript and Nelson Thiffault contributed to the drafts. All co-authors gave final approval for publication. This manuscript will be submitted to the Forest Ecology & Management journal.

3.2 Abstract

Boreal forest regeneration can experience growth interference induced by ericaceous shrub species such as sheep laurel (*Kalmia angustifolia* L.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd). These species have evolved various mechanisms in preventing conifer seedling growth, most noticeably within black spruce (*Picea mariana* (Mill.) B.S.P.) stands. In Quebec, Canada, mechanical scarification is a post-harvest silvicultural practice performed to reduce competition from ericaceous shrubs and has been shown to provide more optimal growing conditions for planted seedlings. However, most long-term studies focus on conifer growth responses, thus, there is a lack of knowledge on the long-term competitiveness of ericaceous shrubs on scarification sites. Additionally, it is believed ericaceous shrubs are more competitive in maritime climates, but few studies compare the competitiveness of ericaceous shrubs in contrasting environments. Our study examines the effectiveness of scarification at reducing the competitiveness and spread of ericaceous shrubs 16-years after treatment within a maritime climate and continental climate. In both climates, scarification resulted in lower total ericaceous shrub cover and lower *K. angustifolia* current year rhizome length compared to non-scarified plots. Within the maritime climate, canopy openness, *K. angustifolia* foliar phenolic concentrations, and *K. angustifolia* foliar nitrogen-use efficiency were lower on scarified plots compared to non-scarified plots. Conversely, *K. angustifolia* foliar nitrogen was lower on non-scarified plots compared to scarified plots. We conclude that scarification successfully reduces ericaceous shrub cover but the benefits from this practice may be greater in maritime climates.

3.3 Introduction

The shift from productive forests to ericaceous shrub dominated sites following disturbances is an issue in boreal forest regeneration. This has been documented in various ecosystems in Europe and North America with species including sheep laurel (*Kalmia angustifolia* L) (Titus et al., 1995), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) (Inderjit and Mallik, 1996), salal (*Gaultheria shallon* Pursh) (Prescott et al., 1996), *Vaccinium myrtillus* L. (Mallik and Pellissier, 2000), *Calluna vulgaris* L. (Hull) (Read and Jalal, 1980), and *Empetrum hermaphroditum* Hagerup (Nilsson and Wardle, 2005). Particularly in eastern Canada, sheep laurel (referred from here as *Kalmia*) can rapidly invade forest sites after disturbances from rapid vegetative regeneration (Mallik, 1993). Lebel et al. (2008) observed sites dominated by *Kalmia* experienced declines in soil fertility and conifer growth rates. Proposed mechanisms for this interference include direct competition for nitrogen (N) due to an extensive root network as well as potential allelopathic effects (Thiffault et al., 2004; Preston, 1999). The suggested allelopathic effects include *Kalmia* phenolics reducing root growth in conifer seedlings as well as reducing ectomycorrhizae-conifer association (Mallik, 1987; Yamasaki et al., 1998). Additionally, high concentrations of condensed tannins found within *Kalmia* litter have negative effects to soil nitrogen cycling (Bradley et al., 2000; Joanisse et al., 2007; Joanisse et al., 2009). Condensed tannins, leached from ericaceous litter, are able to bond with dissolved organic nitrogen within the soil to form stable, recalcitrant tannin-protein complexes (Joanisse et al., 2009; Kraus, 2003). These complexes sequester N which in turn lower N mineralization rates. The decrease in N cycling, thus, leads to an accumulation of recalcitrant humus. (Damman, 1971; Bradley et al., 2000). Decreases to nutrient cycling induced by condensed tannins have also been found to alter forest succession pathways (Schimel et al., 1996). Additionally, ericaceous shrubs are able to access nitrogen immobilized by tannins due to an association with ericoid mycorrhizae (Read, 1996). Therefore, the combination of producing high quantities of condensed tannins

and ability to acquire N through tannin-protein complexes allow ericaceous shrubs to dominate certain sites after disturbances.

It is essential to maintain productivity on sites dominated by ericaceous shrubs in order to support sustainable forest management. Thus, forest management considers various silvicultural options to ensure success. Trench scarification is a type of mechanical site preparation and is performed to enhance conifer seedling establishment. An example of this process is disc trenching, which removes the organic soil layer and the top underlying mineral soil, subsequently depositing the rough mixture overtop the undisturbed forest floor. This results in the formation of a trench, exposing bare mineral soil, which acts as a barrier to ericaceous vegetative expansion (Sutherland and Foreman, 1995; Coates and Haeussler, 1986; Brand, 1991). Conifer seedlings are then planted within the upslope of the trench to provide an optimal seedbed. The trench also provides a buffer area from encroachment by ericaceous shrubs. The objective of this practice is to balance short-term nutrient availability for conifer seedling establishment while preserving longer-term nutrient capital to maintain site productivity (Sutherland and Foreman, 1995). Several studies have reported on the success of scarification in restoring forest regeneration by increasing soil mineralization rates, soil water availability, and soil temperature in the rooting zone (Örlander et al. 1990; Prévost, 1992; Thiffault and Jobidon, 2006).

On sites where scarification is successful, established conifer seedlings will shade out ericaceous shrubs. Although ericaceous shrubs have been found to persist in low light environments, studies on salal have shown that increased shade lead to decreases in growth rate, rhizome production, and aerial stem biomass (Huffman et al., 1994a; Huffman et al., 1994b; Messier, 1992). Therefore, it is expected that the increase in shade would reduce ericaceous shrub above and belowground growth rates, as well as reduce ericaceous shrub cover and litter inputs overtime. Additionally, the decrease in light availability could cause a

reduction in foliar phenolic and condensed tannin concentrations (Bryant et al., 1983; Joanisse et al., 2018). This in turn would produce a higher quality litter that decomposes more readily and releases more N into the soil (Northup et al., 1995; Hättenschwiler and Vitousek, 2000). The combination of reducing ericaceous shrub cover while increasing litter quality would improve soil fertility and promote conifer growth, thus creating a positive feedback loop accelerating canopy closure. Moroni et al. (2009) observed this phenomenon with an increase in canopy closure coinciding with an increase in soil mineralized N and soil total N. Additionally, studies have shown scarification allows conifer seedlings to successfully establish and thereby, surpass ericaceous shrub "growth check" (Tremblay et al., 2013; Thiffault et al., 2010; Thiffault et al., 2017; Johansson et al., 2013).

The majority of studies on long-term scarification effects focus on conifer growth rates and soil fertility. Thus, there is a lack of knowledge regarding the long-term response of ericaceous shrubs to scarification. The mixing of the mineral and organic soil layer can influence the vegetative response depending on the aggressiveness of the competing vegetation (McMinn and Hedin, 1990). Additionally, it is unknown how interactions between scarification and climate regions control the responses of ericaceous species. It is believed that site conditions may alter the competitive ability of ericaceous shrubs. Maritime climates may be more favorable for ericaceous species due to slower soil decomposition rates in cool humid environments (Swift et al., 1979). These conditions lead to a decrease in soil microbial activity which decreases decomposition rates. This results in an accumulation of thick lignin-rich forest floors that would support the spread and dominance of ericaceous shrubs. This may be explained by ericaceous species emergence and survival favoring moist woody substrates compared to mineral soil as seen with salal (Huffman et al., 1994b). Additionally, there is a contrast in the consideration of ericaceous shrubs between maritime climates versus continental climates. Maritime provinces in Canada have observed an unexpected appearance of *Kalmia* heathlands after disturbances such as wildfire and clearcutting (Hall et al., 1973; Meades, 1983). Conversely, management in Western Ontario have seldom reported forest

regeneration issues caused by ericaceous species but rather considered ericaceous shrubs as beneficial to wildlife habitat (Ministry of Natural Resources North Bay District, 2002; Walker, 2001; Baycroft, 2001) Therefore, varied responses by ericaceous shrubs to scarification may be expected in contrasting environments, which would alter management strategies.

Our objective was to test for the interactions between scarification and climate regime controlling the long-term responses of ericaceous shrubs. We hypothesized that scarification would accelerate canopy closure and decrease ericaceous shrub competitive ability. We further hypothesized that scarification would reduce the competitive ability of ericaceous shrubs more so in a drier continental regime than in a humid maritime regime. To test these hypotheses, we conducted a study where we measured above ground spread of ericaceous shrubs, foliar and rhizomatous traits, canopy openness, and forest floor N mineralization rates in 16 year old black spruce stands. One stand was located in a continental climate regime in western Quebec and the other stand was located in a maritime climate regime in eastern Quebec. Scarification was performed on plots with adjacent non-scarified plots (each pair considered as blocks) at both stands.

3.4 Materials and Methods

Study sites and regions

Scarification trials were established in 1999 in two climatic regions (Fig. 3.1) (Thiffault et al., 2005; Thiffault and Jobidon, 2006). One site was established in the Côte-Nord region of

Quebec, north of the city of Baie-Comeau, in the black spruce (*Picea mariana* (Mill.) BSP) – feathermoss bioclimatic domain (49°47 18′ ″N, 69°17 12′ ″W) described by Saucier et al.

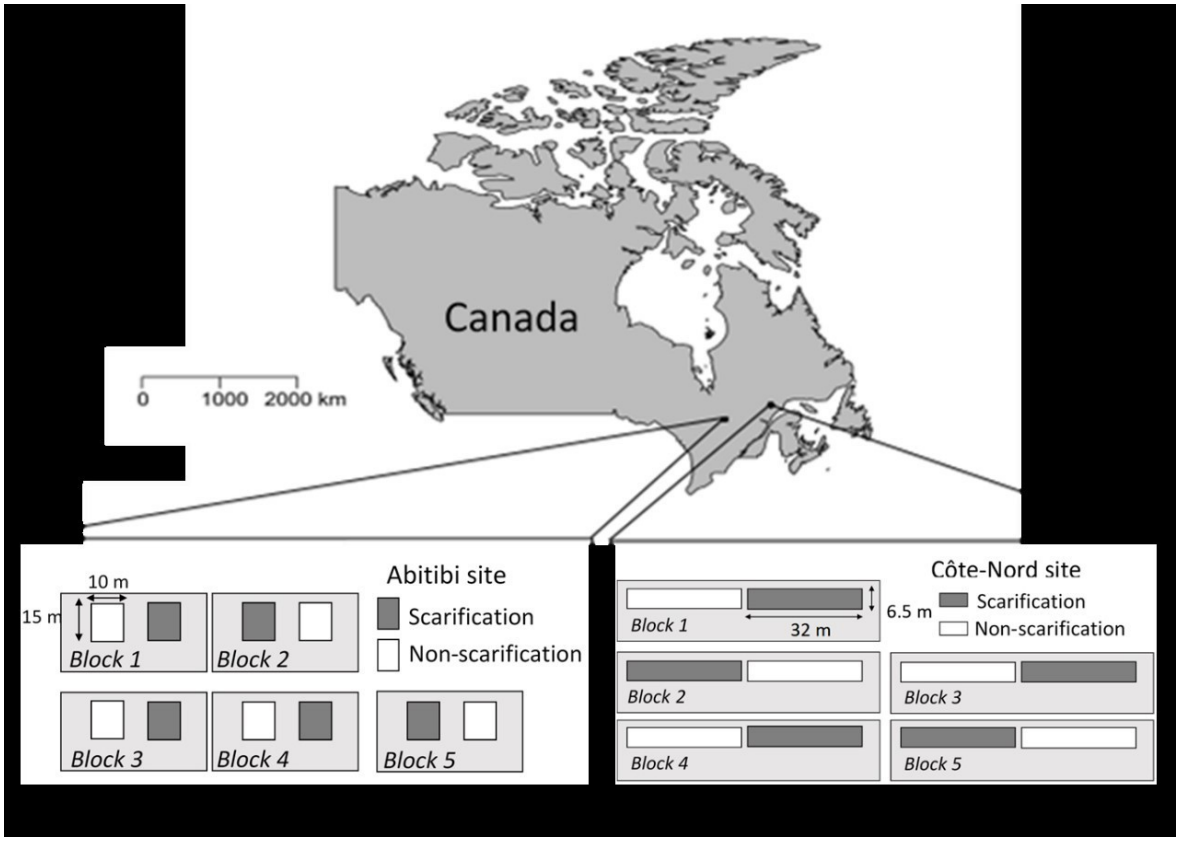


Figure 3.1 Location of scarification trials established in 1999 by a randomized split block design of scarified and non-scarified (control) plots in Abitibi and Côte-Nord, Quebec, Canada.

(2009). The Côte-Nord region is characterized by a mean annual temperature of -1.0 °C with a growing season of ca. 140 days., mean annual precipitation of 1300 mm (35 %-45 % falls as snow), and a 18 cm deep mor humus (Saucier et al., 2009; Soil Classification Working Group, 1998). This site will be referred to as "Côte-Nord" and is considered the "maritime climate". The second site was established in the Abitibi region of Quebec, northeast of the town of Senneterre, within the balsam fir (*Abies balsamea* (L.) Mill) – white birch (*Betula*

papyrifera Marsh.) bioclimatic region (Saucier et al., 2009). The Abitibi region is characterized by a mean annual temperature of 2.5 °C with a growing season of ca. 150-160 days, mean annual precipitation of 950 mm (30% falls as snow), and a 8 cm deep mor humus (Saucier et al., 2009; Soil Classification Working Group, 1998). The site will be referred to as "Abitibi" and is considered the "continental climate". Both sites are characterized by a Humo-Ferric Podzolic soil (Soil Classification Working Group, 1998) formed from moderately well drained glacial till with a sandy loam texture (74% sand, 22% silt, 4% clay) in the first 15 cm (Thiffault et al., 2005; Thiffault and Jobidon, 2006)

The Côte-Nord site was clear-cut in 1993, and had supported a black spruce stand over 120 years old. Following harvest, the site developed a dense cover of ericaceous shrubs, dominated by *Kalmia* and Labrador tea. The Abitibi site was clear-cut in 1999 and had supported a 70 year old stand that originated after wildfire and was composed of black spruce and jack pine (*Pinus banksiana* Lamb.). Following harvest, the site developed an evenly distributed cover of *Kalmia*, *Vaccinium* spp., and ground lichens (*Cladina* spp.). The contrasting water regime at the two sites induced a striking difference in ground cover, with a higher lichen cover in Abitibi and higher moss cover in Côte-Nord.

Both experiments consisted in randomized block designs that notably included a scarification treatment (TTS passive disc trencher) and a control (no scarification), randomly applied within ten replicate blocks (Thiffault et al., 2005; Thiffault and Jobidon, 2006). Plots were 6.5 m x 32 m with 2 m buffer zones in Côte-Nord, and 15 m x 10 m with 6 m buffer zones in Abitibi. Containerized black spruce seedlings grown for two years from local seed sources were planted according to a 2 m x 2 m grid at both sites in June 2000.

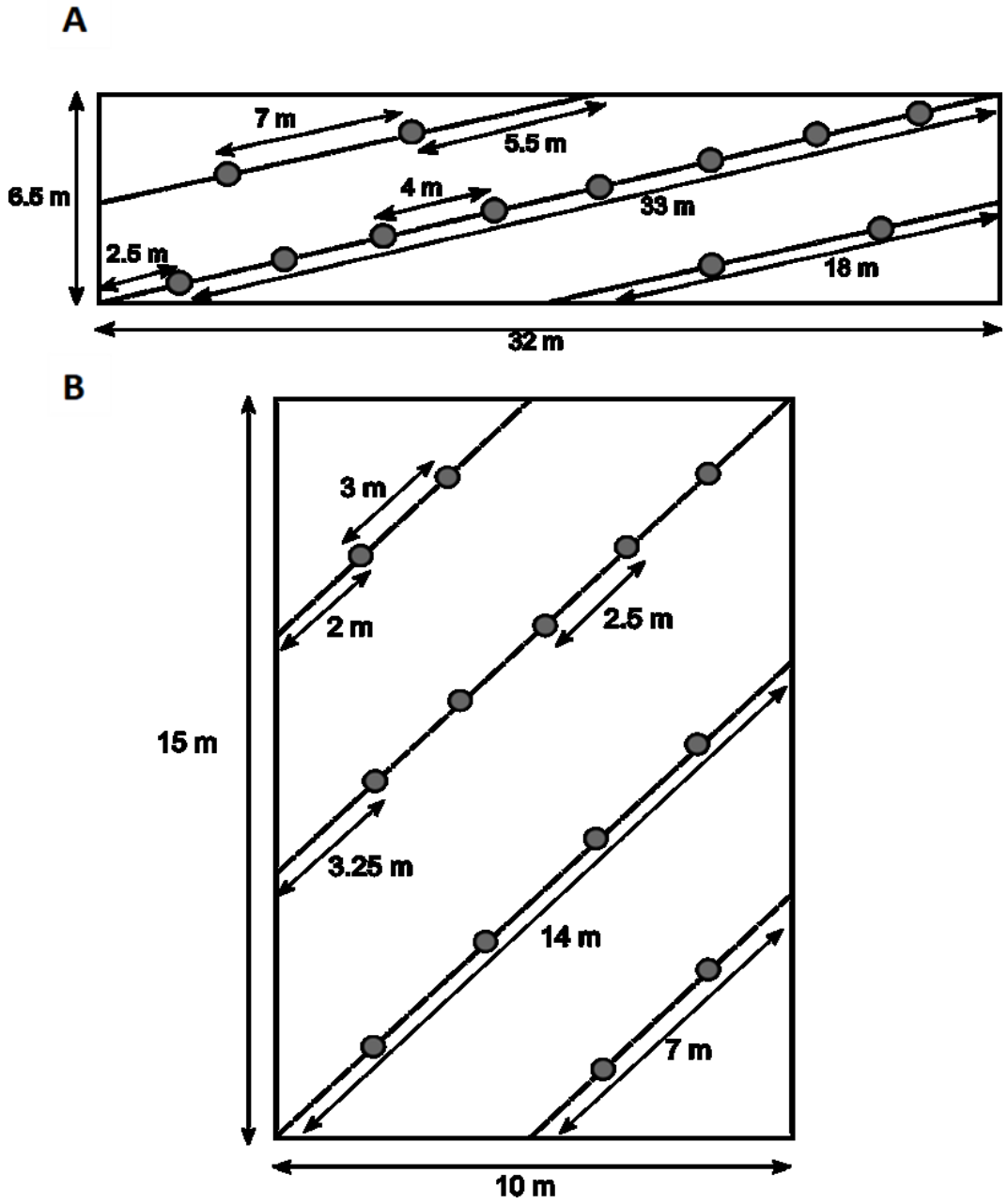


Figure 3.2 **Experimental design for plots with established transects in Côte-Nord (A) and Abitibi (B). Dotted lines represent transect lines with dimensions and spacing indicated by lined arrows. Grey points represent sampling locations.**

Field sampling

In early June of 2016, we chose five replicate blocks in each region to conduct our study (for a total of 20 plots). We established, at each site within the 10 plots, diagonal transects along which we distributed 12 sampling points. The number and length of the transects were adapted based on the size of the plots of each site (Fig. 3.2A and 3.2B). At the twelve sampling points of each plot, we took a hemispheric photo of the canopy at 1 m height using a Nikon fisheye converter FC-E8 0.21x lens attached to a Nikon Coolpix 5000 camera in mid-July 2016. Additionally, the observer visually estimated the percent ground cover of understory shrubs, lichen, and moss within a 1 m radius.

At three sampling periods throughout the 2016 growing season (mid-July, end of August, and mid-September), 5 L samples of organic soil F-layer material (Soil Classification Working Group, 1998) were collected at each sampling point within a plot and divided into 2 bulk samples (each bulk sample contained soil from 6 sample points). Samples were sieved on site through 5 mm wire mesh, transferred into sealed plastic bags, placed under ice packs in coolers, transported to the *Laboratoire d'écologie des sols* (U. Sherbrooke), and stored at 4 °C until analyzed.

At the end of August 2016, current and second-year *Kalmia* and Labrador tea leaves were collected, separately, at each sampling point (but Labrador tea was absent from the Abitibi site). These were transported to the *Laboratoire d'écologie des sols* (U. Sherbrooke) in coolers and stored at 4 °C until analyzed. At the beginning of June 2016, in each of the 20 plots, four 1 m^2 litter traps per plot were placed under both *Kalmia* and Labrador tea patches (where applicable). Leaf litters were collected from each litter trap in mid-September 2016,

sorted by species, transported in paper bags to the *Laboratoire d'écologie des sols* (U. Sherbrooke), and stored at 4 °C until analyzed.

At the end of August 2017, we collected current-year *Kalmia* rhizomes from each plot. To do this, we removed the moss or lichen cover down to the organic forest floor F layer using a cultivator rake and carefully scraped through the forest floor until laterally growing current-year rhizomes were identified. Rhizomes were identified by their characteristic pink-white flesh and apical meristem, and older suberized portions were followed back to the source shrub for species verification. Twenty to thirty rhizomes were collected at each plot and the length and total number of vegetative buds along each rhizome were measured immediately after collection. These were transported to the *Laboratoire d'écologie des sols* (U. Sherbrooke) in coolers and stored at 4 °C until analyzed.

Laboratory analyses

We uploaded canopy photos into Gap Light Analyser (Version 2.0) software from each sampling point to estimate canopy openness (Frazer et al., 1999). We averaged the 12 photos per plot to yield a single canopy openness value per plot. Aerobic incubations were used to measure mineralizable N in the bulk forest floor samples from the three sampling periods. To do so, we transferred duplicate 5 g (dry wt. equiv.) subsamples into mason jars, covered them with polyethylene film and incubated them at room temperature for 30 days. We extracted the subsamples with 50 mL of 1 M KCl aqueous solution, filtered the forest floor solution through Fisherbrand™ P5 filter paper, and analyzed the filtered solution colorimetrically for NH_4^+-N (salicylate–nitroprusside-hypochlorite) using an Astoria 2 Analyzer (Astoria Pacific Inc., Clackamas, OR, USA). We measured the surface area of 100 current and second-year *Kalmia* and Labrador tea leaves from each plot using a digital scanner interfaced with the

software program WinFOLIA (V 2001 a) (Regent Instruments Inc., Québec City, QC, Canada). To calculate specific leaf area (SLA), we freeze dried all of the leaves and weighed the dry-mass. We also calculated specific rhizome mass (SRM) by dividing the total oven dry (65 °C) mass of rhizomes by total rhizome length. We oven dried (65 °C) the forest floor samples from the three sampling periods. We ground all of the leaf, litter, and forest floor samples to a fine powder using a Retsch model MM200 ball mill (Retsch GmbH & Co., Haan, Germany), encapsulated 80-100 mg of ground subsamples in Sn and analyzed these for total C and N by high temperature combustion and thermo-conductometric detection, using a Vario Macro dry combustion analyzer (Elementar Analysensyteme GmbH, Hanau, Germany). We calculated foliar % N resorption efficiency of *Kalmia* and Labrador tea using current year foliar N concentration and litter N concentration in the equation (Chapin and Kedrowski, 1983):

$$\text{Foliar \% N resorption efficiency} = \frac{[Nitrogen]_{current-year} - [Nitrogen]_{litter}}{[Nitrogen]_{current-year}} \times 100\%$$

Equation 3.1 Foliar % N resorption equation as an index of N use efficiency.

Finally, we analyzed *Kalmia* and Labrador tea foliar and litter total extractable phenolics by the Folin-Ciocalteu assay, and for condensed tannins by the butanol-HCl assay (Waterman and Mole, 1994; Preston, 1999). We extracted 10-15 mg aliquots of ground leaf and litter subsamples with 10 mL of acetone:water (70:30). Total phenolics were standardized against tannic acid (Fisher Scientific) and tannins were standardized against purified *Kalmia* condensed tannins (Preston, 1999).

Statistical analyses

Mixed model two-way ANOVAs were used to test the effects and possible interactions of treatment (i.e. scarification vs control) and site (i.e. Côte-Nord vs. Abitibi) on each of the response variables, with block coded as a random effects variable. When significant interactions were found, one-way mixed model ANOVAs were used to test the effect of scarification treatment within each individual site, with block coded as a random effects variable. Whenever significant effects were found, a post-hoc Tukey's HSD test was performed for multiple comparisons of means. Prior to analyses, all data were verified for normality and homogeneity of variance assumptions, and the level of significance for all tests was set to $P \leq 0.05$. All statistical analyses used the function *lmer* of the package *lme4* in R v.3.4.2 software (Bates et al., 2015; R Core Team, 2017).

3.5 Results

Canopy openness and ericaceous shrub cover

There was a significant ($P < 0.001$) interaction between site and scarification controlling canopy openness (Fig. 3.3). Non-scarified plots in Côte-Nord had significantly greater canopy openness (72.2%) ($P < 0.001$) than scarified plots (59.2%). Abitibi plots had no significant difference in canopy openness between non-scarified (58.6%) and scarified (57.2%) plots.

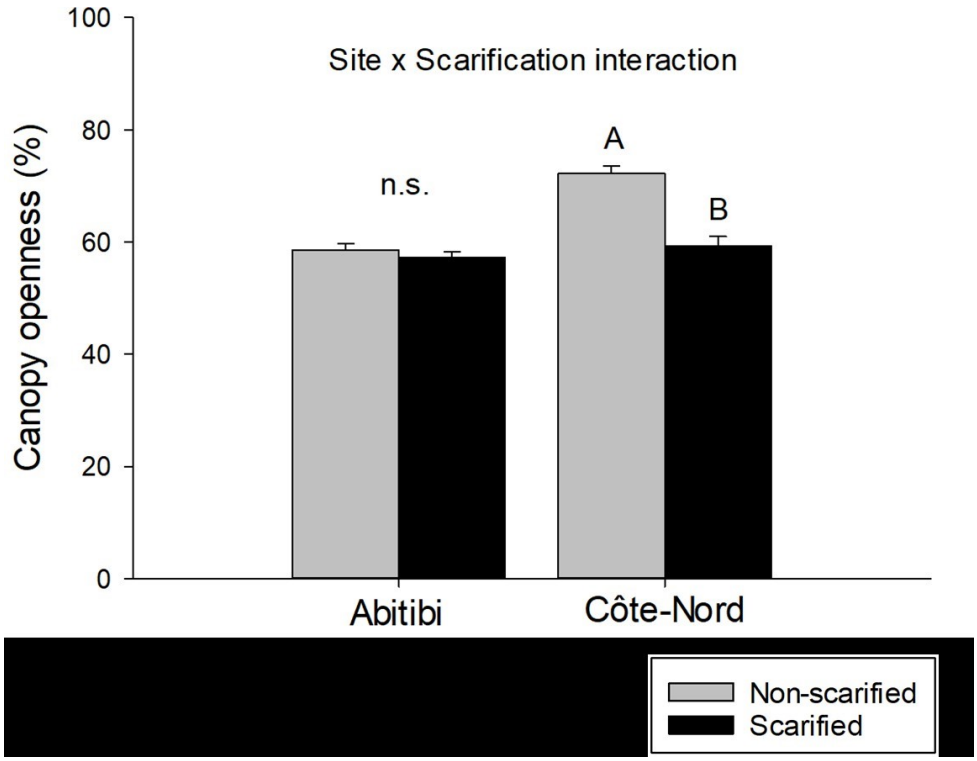


Figure 3.3 **Average canopy openness on scarified (black bars) and control plots (grey bars) at both sites. Text at the top of the frame reports a significant Site x Scarification interaction. Different upper-case letters indicate significant differences between treatments within a given site. Vertical lines = 1 S.E**.

There was a significant (P = 0.023) interaction between site and scarification controlling *Kalmia* cover (Fig. 3.4A). Non-scarified plots (20.5 %) in Abitibi had significantly (P < 0.001) higher *Kalmia* cover than scarified plots (11.6 %) but there was no significant scarification effect in Côte-Nord (18.1 % on non-scarified plots and 14.7 % on scarified plots). Labrador tea was only present in Côte-Nord and cover was significantly (P = 0.039) higher on non-scarified plots (19.8 %) than scarified plots (11.3 %) (Fig. 3.4B). There was a significant (P = 0.007) interaction between site and scarification controlling *Vaccinium* cover (Fig. 3.4C). Scarified plots in Côte-Nord had significantly (P = 0.009) higher *Vaccinium*

cover (4.1%) than non-scarified plots (1.8%). Across the two sites, non-scarified plots (36.7 %) had significantly ($P < 0.001$) higher total ericaceous shrub cover than scarification treatment (26.5 %) (Fig. 3.4D). Additionally, Côte-Nord (34.9 %) had significantly ($P = 0.005$) more total ericaceous cover than Abitibi (28.3 %).

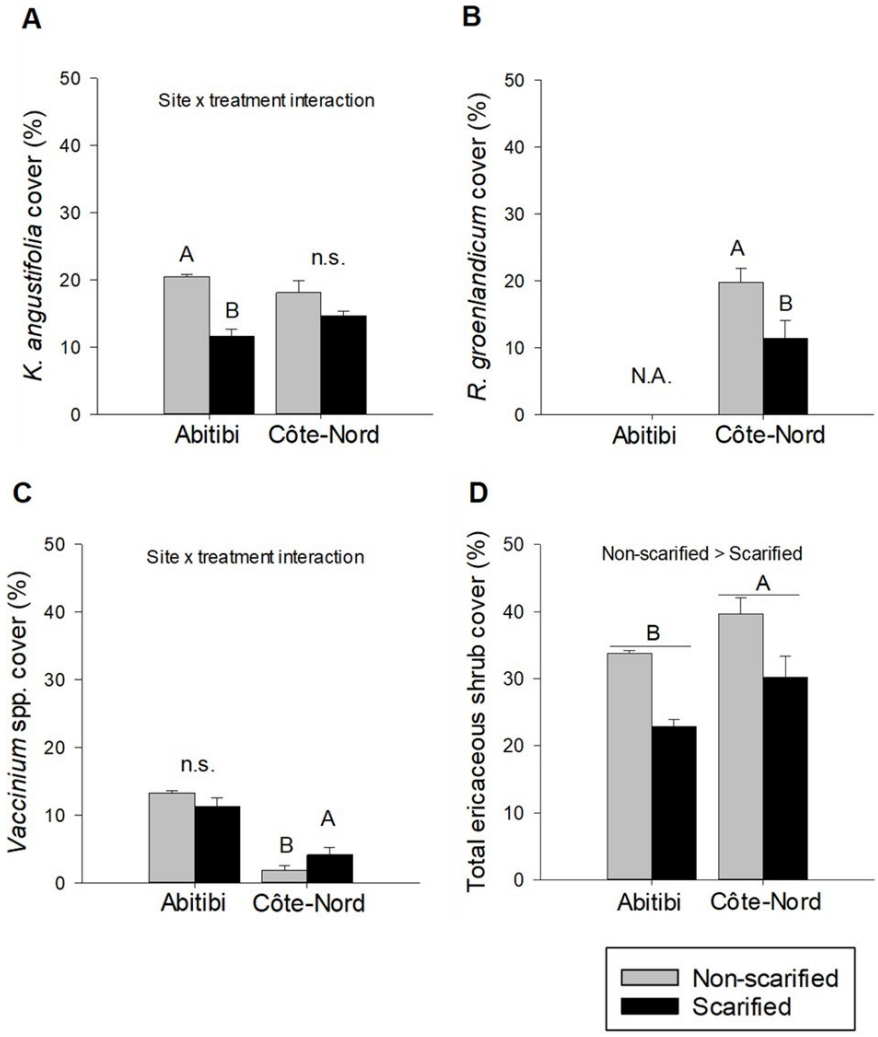


Figure 3.4 **Average ericaceous shrub cover on scarified (black bars) and control plots (grey bars) at both sites. The four frames report the average cover of *K. angustifolia* (A), *R. groenlandicum* (B), *Vaccinium* spp. (C), and total ericaceous shrubs (D). Text at the top of the frame reports a significant Site x Scarification interaction or main effects of treatment. Different upper-case letters indicate significant differences between treatments within a given site. Different upper-case letters above a horizontal line indicate differences between sites. Vertical lines = 1 S.E.**

Kalmia *rhizomes*

There was a significant ($P < 0.001$) interaction between site and scarification controlling rhizome length (Fig. 3.5A). Specifically, non-scarified plots had significantly longer rhizomes than scarified plots in Côte-Nord (9.7 cm and 6.1 cm respectively) ($P < 0.001$) and Abitibi (7.4 cm and 6.5 cm respectively) ($P = 0.004$). Additionally, there was a significant ($P = 0.017$) interaction between site and scarification controlling SRM (Fig. 3.5B). Non-scarified plots (6.4 mg cm^{-1}) had significantly ($P = 0.002$) higher SRM than scarified plots (4.5 mg cm^{-1}) in Côte-Nord.

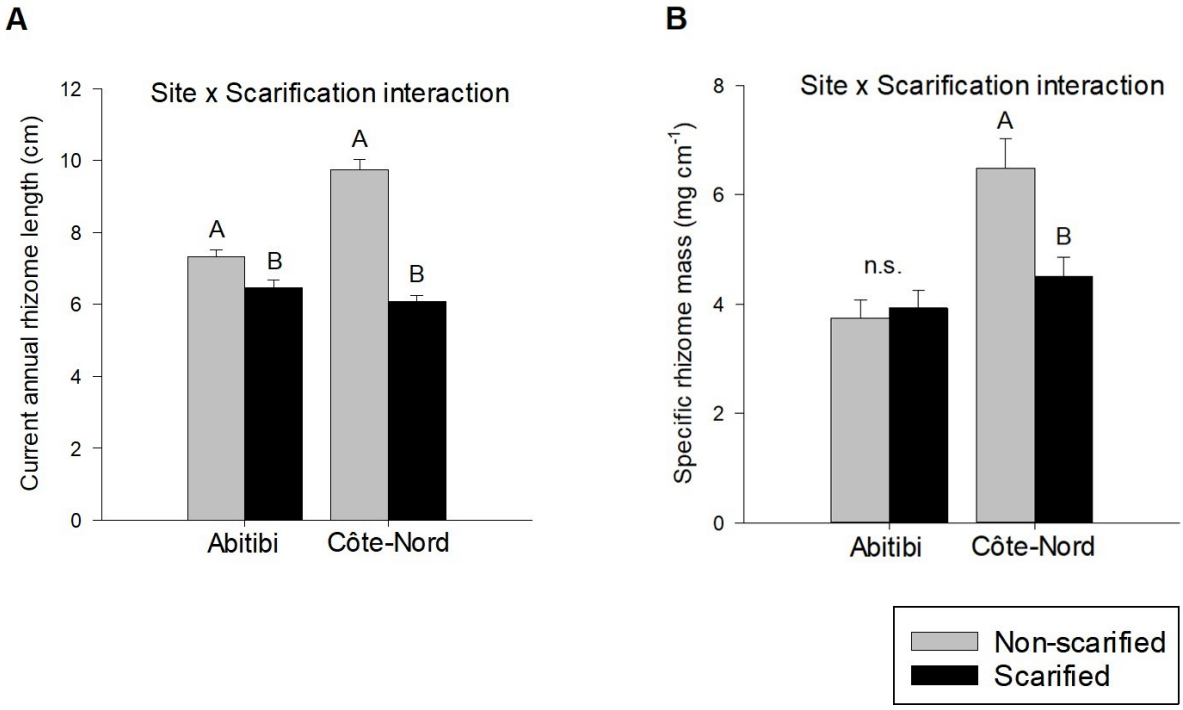
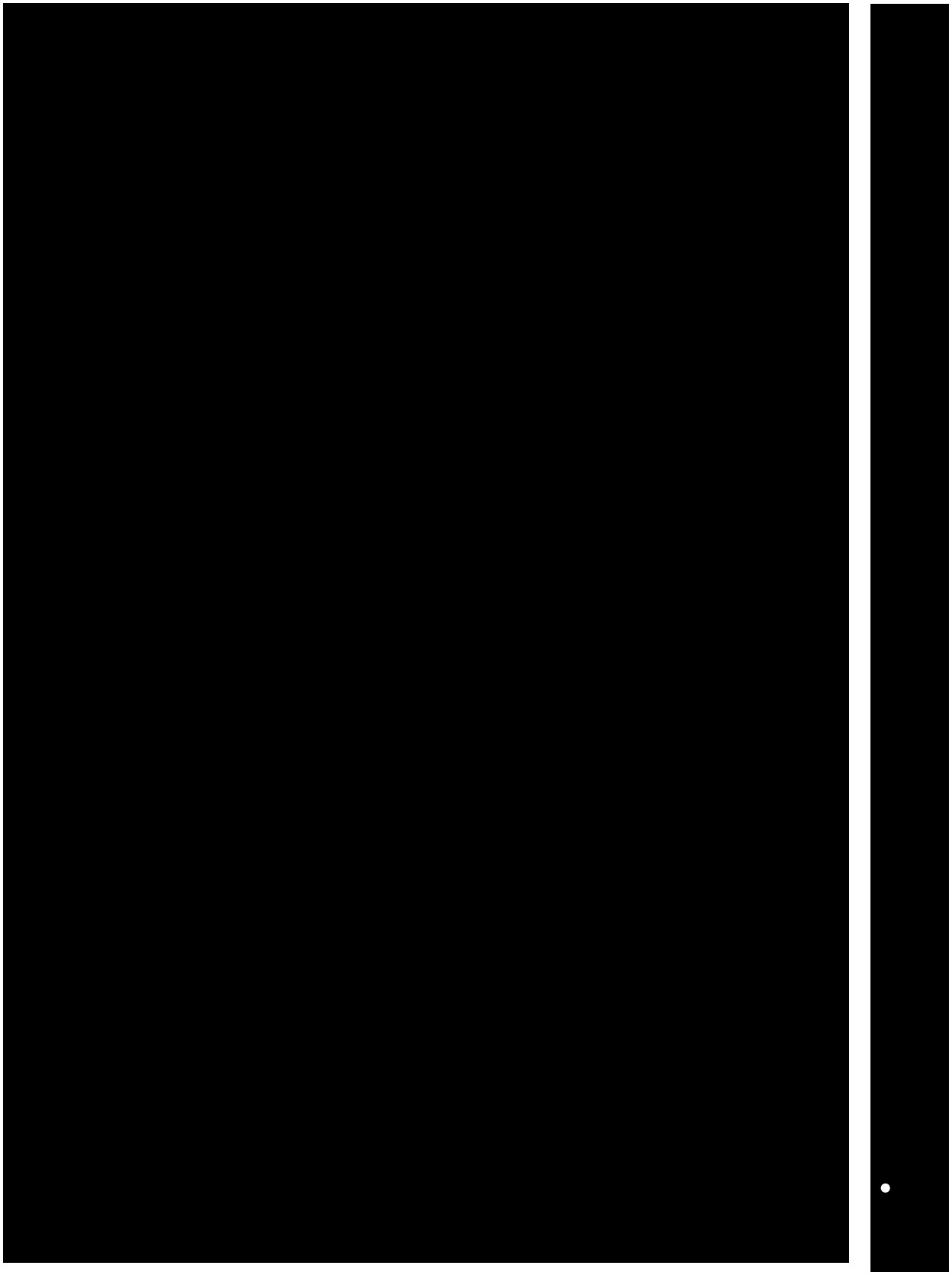


Figure 3.5 **Average current annual rhizome length (A) and specific rhizome mass (B) on scarified (black bars) and control plots (grey bars). Text at the top of the frame reports a significant Site x Scarification interaction. Different upper-case letters indicate significant differences between treatments within a given site. Vertical lines = 1 S.E.**

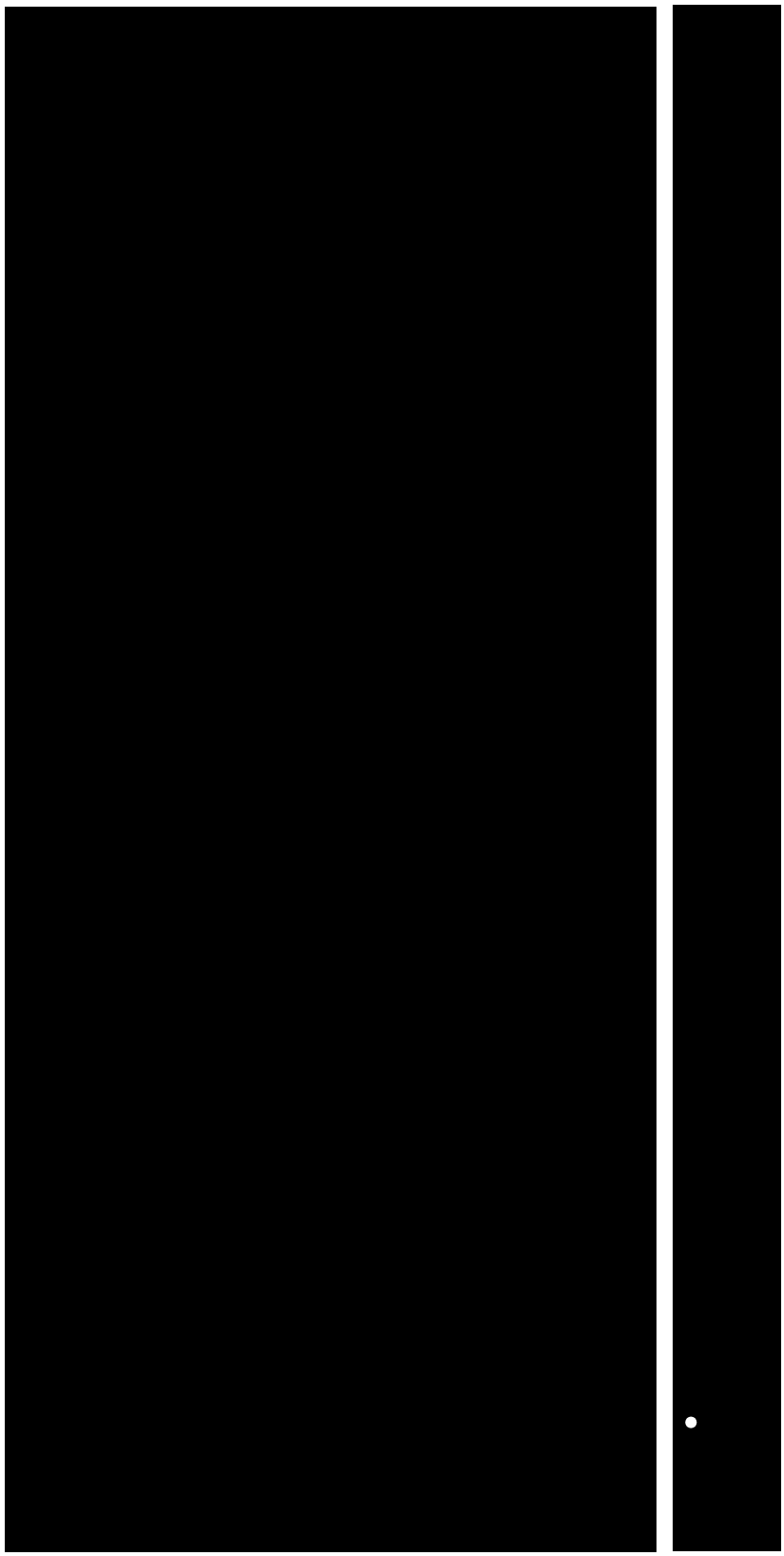
Kalmia *and Labrador tea foliar properties*

There were significant interactions between site and scarification controlling *Kalmia* litter total phenolics ($P = 0.044$), between site and scarification controlling *Kalmia* second-year foliar N ($P = 0.035$), and between site and scarification controlling *Kalmia* litter N ($P = 0.036$) (Table 3.1). In Côte-Nord, total phenolics in *Kalmia* litter and *Kalmia* current year leaves were significantly higher on non-scarified plots than scarified plots ($P = 0.018$, $P = 0.013$). *Kalmia* current and second year foliar C:N ratio ($P = 0.024$, $P = 0.003$), *Kalmia* litter C:N ratio ($P = 0.006$) and Labrador tea litter C:N ratio ($P = 0.005$) were significantly higher on non-scarified plots than scarified plots in Côte-Nord. Additionally in Côte-Nord, *Kalmia* % N resorption ($P = 0.0017$) and Labrador tea % N resorption ($P = 0.034$) were significantly higher on non-scarified plots than scarified plots. Conversely, *Kalmia* litter N and *Kalmia* current and second-year foliar N ($P = 0.037$, $P = 0.002$, $P < 0.001$), *Kalmia* current and second-year foliar SLA ($P = 0.013$, $P < 0.001$), Labrador tea second-year foliar N ($P = 0.026$) and Labrador tea litter N ($P = 0.006$) were significantly higher on scarified plots compared to non-scarified plots in Côte-Nord. Additionally, *Kalmia* litter C:N ratio, was significantly higher on non-scarified plots than scarified plots in both Côte-Nord ($P = 0.006$) and Abitibi ($P = 0.047$). Overall, non-scarified plots had significantly higher *Kalmia* % N resorption ($P = 0.004$), and *Kalmia* litter C:N ratio ($P < 0.001$) compared to scarified plots. *Kalmia* current and second year total phenolics ($P = 0.025$, $P = 0.001$), *Kalmia* current and second-year foliar N ($P = 0.008$, $P = 0.045$), and *Kalmia* litter N ($P = 0.017$) were significantly higher in Côte-Nord than Abitibi. Conversely, *Kalmia* current and second-year foliar C:N ratio ($P = 0.012$, $P = 0.012$), *Kalmia* second-year foliar SLA ($P = 0.029$), and *Kalmia* litter total phenolics ($P = 0.024$) were higher in Abitibi compared to Côte-Nord.



Forest floor N-mineralization

The organic soil samples had mineral soil mixed within due to the scarification process. The additional mineral soil would bias the samples from the difference in density in comparison to samples without mineral soil. To accommodate the differences in density due to mineral soil between scarified and non-scarified treatments, we report N-mineralization on a per gram total N versus per gram of soil. N-mineralization was higher on scarified plots for each sampling period as well as the seasonal average in Côte-Nord and Abitibi but was not statistically significant (Table 3.2). N-mineralization was higher in Côte-Nord than Abitibi in the mid-July sampling period ($P = 0.030$).



3.6 Discussion

We acknowledge the lack of replicated sites within each climate region which precludes statistical inferences about the climate regime explaining the differences between the sites. However, given that the sites had similar drainage, till deposit, tree age and species, ericaceous shrubs, and similar scarification, we believe the main factor differentiating the sites was climate and thus, we cautiously used the climate variable within our interpretation. Therefore the following discussion will assume climate as an explanatory variable.

Canopy openness

Canopy openness is an indicator of the progress and the current state of conifers shading out ericaceous shrubs. It is a relative proxy for interpreting conifer radial growth and natural conifer regeneration. Overstory cover from other species, such as *Alnus incana* subsp. *rugosa* (Du Roi) R.T. Clausen, was very low, therefore, the canopy cover from our measurements is mostly from conifer canopy cover. The different canopy responses in the two climate regimes indicate that scarification has allowed conifer seedlings to overcome growth check from ericaceous shrubs more so in the maritime climate. Scarified plots in Côte-Nord had a lower canopy openness in comparison to control plots. This successful radial growth from the planted conifer seedlings and natural conifer regeneration can potentially be attributed to the trench buffer zone preventing encroachment by ericaceous shrubs. Conversely in the continental climate, both control and scarified plots had similar canopy openness to the scarified plots in Côte-Nord. This could be attributed to similar radial growth from planted seedlings as well as natural conifer regeneration on the control plots and scarified plots. However, previous scarification studies have shown planted conifer seedlings on scarified plots had greater growth rates compared to planted conifer seedlings on control

plots. Therefore, canopy openness does not reflect conifer growth rate or conifer size. If conifer growth rate from planted seedlings is greater on scarified plots compared to control plots, then the similar canopy openness that we observed may be explained by natural conifer regeneration. This may occur in the continental climate because of a thinner organic soil layer and higher growing season temperatures compared to the maritime climate. Greater soil temperatures increase seedling growth and survival by influencing such processes as respiration and water uptake by roots. Thus, natural conifer regeneration may occur on control plots as well as scarified plots (Örlander, 1990).

Spread of ericaceous shrubs

A key objective of scarification is reducing the competition of ericaceous shrubs by creating zones that are free of organic forest floor material. Ericaceous shrub rhizomes preferentially grow within the organic soil layer, where they have been observed to rapidly regenerate following a disturbance (Mallik, 1993). By creating a trench of bare mineral soil through the scarification process, the disruption to the organic layer prevents ericaceous shrub rhizomes from spreading. Several studies have documented this phenomenon in the years immediately following treatment (Mallik and Kravchenko, 2016; Thiffault and Jobidon, 2006; Thiffault et al., 2005; Nilsson et al., 2006). However, it is unknown how rhizome growth responds to the mixing of organic and mineral soil within the berms. Additionally, over time a thin organic layer within the trench would form, potentially leading to the invasion of ericaceous shrubs. As the growth of rhizomes controls the number of new shoots sprouting from rhizome buds, understanding rhizome responses to scarification will inform us on the efficiency of scarification.

The interaction between treatment and sites controlling rhizome length may indicate a combination of light intensity and the mixing of organic and mineral soil influence. Rhizome length response was greater in Côte-Nord on non-scarified plots, which also had greater canopy openness compared to scarified plots. This may indicate that longer rhizomes be due to greater light availability. This is in agreement with studies on salal that found rhizome growth declines with increasing shade (Huffman et al., 1994a; Messier, 1992). This indicates that the accelerated canopy closure due to scarification can successfully decrease rhizome growth which will limit the spread of ericaceous species. However, shorter rhizomes were also observed on scarified plots in Abitibi despite there being no difference in canopy openness between scarified and non-scarified plots. This may indicate that the mixing of the organic and mineral soil may influence rhizome length in addition to light availability. The mixed soil may reduce rhizome length because *Kalmia* rhizomes preferentially grow within the organic soil layer (Mallik, 1993). Pockets of mineral soil within the mixed soil may act as a cue that rhizomes are growing out of the organic soil layer. This would deter rhizomes from continuing to grow into this medium because it would not be beneficial for nutrient acquisition (Read et al., 2004). Overall this would reduce the mean rhizome length of the plot. Although the difference between treatment and control was minimal (1 cm), this could result in a larger difference in total rhizome length over time. As we observed no difference in number of buds per rhizome length, shorter rhizomes would provide fewer buds for shoots to sprout. This is a possible advantage of scarification in addition to reducing rhizome growth by increased shade.

We observed higher specific rhizome mass (SRM) and higher canopy openness on non-scarified plots compared to scarified plots in Côte-Nord. However in Abitibi, there was no difference in SRM nor in canopy openness. Thus in comparison to rhizome length, specific rhizome mass (SRM) may be influenced more so by light availability. SRM is the reciprocal of specific root length (SRL). SRL provides a ratio of the root length to root mass. This measurement is beneficial for examining the economic aspects of a plant's root system

acquiring nutrients. However, the primary role of ericaceous shrub rhizomes is to produce new stems, not necessarily acquiring nutrients. Therefore, SRM is a useful measurement to examine the benefit-to-cost index of rhizomes because it represents the carbon storage within rhizomes available to shoots to sprout from vegetative buds. Studies have found that *Kalmia* had the highest photosynthetic rate at full sunlight and decreased with increasing shade (Mallik et al., 2012). The higher photosynthetic rate would produce more available carbon to allocate to rhizomes, thus increasing SRM. The additional carbon storage provides the bud bank with greater resources for shoots to sprout. Therefore, the increase in shade may reduce the ability of ericaceous shrubs to increase cover by reducing carbon resources available to sprouting shoots.

In the maritime climate and the continental climate, ericaceous shrub cover was greater on control plots compared to scarified plots. This may reflect that the trenches, created by scarification, have an insufficient amount of organic soil material for ericaceous species to proliferate through. It has been proposed that the disturbance from disc trenching may stimulate regeneration of woody shrubs (Sutherland and Foreman, 1995), and Thiffault et al. (2005) documented rapid *Kalmia* ingrowth following disc trenching. This reflects ericaceous species ability to proliferate after disturbances (Mallik, 1993). However, the lower ericaceous shrub cover on scarified plots suggest that the trenches may continue to prevent the encroachment of ericaceous species.

Scarification driving a positive feedback loop between improving soil fertility and accelerating canopy closure

Creating conditions that allow conifer growth rates to increase is one component of scarification which can be aided by improving the litter quality of ericaceous species which

in turn will improve soil fertility (Lortie and Aarssen, 1996). We hypothesized that scarification would accelerate canopy closure which in turn would shade out ericaceous shrubs. This in turn would alter ericaceous foliar properties and improve ericaceous litter quality and lead to improved soil fertility. The improved nitrogen cycling would then increase conifer growth rates and the rate of canopy closure. Our study supports elements of this positive feedback loop, most notably, from the decrease of phenolics within *Kalmia* current and second year leaves and *Kalmia* litter on scarified plots in Côte-Nord. This can be attributed to the carbon-nutrient balance theory which suggests that plants allocate carbon to secondary chemicals in conditions when carbon exceeds other nutrient and growth demands (Bryant et al., 1983). Thus as the canopy closes, it would be expected that *Kalmia* produces less carbon to be allocated to phenolics. Ericaceous shrubs have been shown to decrease photosynthetic rates with increasing shade, which in turn would produce less carbon (Mallik et al., 2012; Hebert et al., 2010). Additionally, studies have found a decrease in phenolic and condensed tannin production by ericaceous shrubs with decreasing light availability (Joanisse et al., 2018; Hofland-Zijlstra and Berendse, 2008; Iason and Hester, 1993). Thus, it is expected that reducing secondary metabolites would improve conifer growth by increasing N-mineralization rates (Bradley et al., 2000). Although we found no statistically significant difference in N-mineralization between scarified and control plots, we note that within each sampling period as well as the seasonal average, N-mineralization was higher on scarified plots than non-scarified plots in both Côte-Nord and Abitibi. If this trend holds true, then scarified plots may have a higher soil fertility which in turn would promote conifer growth more so than control plots. The lack of statistical difference may be because of the necessity to report N-mineralization on a total N basis. Reporting N-mineralization on a per gram of soil is unreliable due to the mixed soil on scarified plots and obtaining total N on a per area basis is too difficult because of the heterogeneous nature of the scarified soil. Thus, the lack of statistical difference between N-mineralization on scarified and control plots may reflect the large variation between samples from reporting on a total N basis.

There is other evidence that scarified plots are more fertile than non-scarified plots and more so in Côte-Nord. *Kalmia* and Labrador tea on scarified plots in Côte-Nord had higher foliar N and a lower % N resorption (an indication of N-use efficiency) compared to non-scarified plots. This suggests that scarified plots have a higher soil fertility than control plots. Previous studies have found plants conserve nutrients more efficiently on nutrient-poor substrates by re-allocating foliar N from senescing leaves. By resorbing foliar N before litterfall, the plant is less dependent on environmental nutrient supply (Aerts, 1996; Vitousek, 1982; Boerner et al., 1984). Ericaceous shrubs on scarified plots were less N-use efficient but had a higher foliar N concentration, suggesting that scarified plots have a higher soil N availability. Additionally, the lower C:N ratio within *Kalmia* and Labrador tea litter would contribute to increasing site fertility. Litter with lower C:N ratio typically decomposes faster and contributes more nitrogen to the soil compared to higher C:N litter ratios (Coulson and Butterfield, 1978; Berg and Staaf, 1980; Taylor et al., 1989). Interestingly, scarified plots in Abitibi also had a lower *Kalmia* litter C:N ratio despite both scarified and control plots having the same canopy closing process occurring. This may be an indication that even with similar canopy openness, scarified plots have a higher soil fertility. Several *Kalmia* foliar variables in Abitibi follow the same trends as that found in the maritime climate with lower foliar phenolic concentrations, higher foliar N, and lower foliar % N resorption found on scarified plots. It is only that litter C:N ratio was found to be significant. Therefore the more readily decomposable litter in both climate regimes would contribute to a positive feedback loop by increasing soil fertility.

As the canopy closes, shade will increase ericaceous shrub foliar SLA in order for the leaves to increase the efficiency of light capture. We observe this morphological change on scarified plots in Côte-Nord in which both *Kalmia* current and second year leaves had higher SLA compared to non-scarified plots. Thus, SLA, foliar N and arguably soil N-mineralization increased in Côte-Nord due to scarification. This suggests the litter quality is higher on

scarified plots which will improve site quality. This effect was not as strong in Abitibi, most likely because of the similar leaf morphology between control and scarified plots.

Management implications

Our study confirms that scarification reduces the competitive ability of ericaceous shrubs but more so in the maritime climate than in the continental climate. This gives evidence of the benefits of scarification in maritime climates from the continuous improvement to site fertility. Conversely in continental climates, the similar canopy openness between scarified and control plots indicate a comparable stage in shading out ericaceous shrubs. Although this indicates that control plots may experience the benefits of shading out ericaceous shrubs, it does not mean scarification is unnecessary. Scarification is performed to optimize conifer growth and establishment, therefore to achieve this objective, this practice should still be performed. Overall, the numerous amount of interactions observed between the contrasting sites indicates the necessity of different management strategies based on climate regime. Future research efforts should incorporate multiple sites within climate zones. This will provide more robust support to our conclusions and will enable to establish threshold values of ericaceous shrub cover at which conifer growth check is alleviated.

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CHAPTER 4

GENERAL DISCUSSION AND CONCLUSION

The objective of our project was to test several hypotheses regarding the interaction between silvicultural practices and climate regime/soil deposit controlling ericaceous species responses. In Chapter 2, we hypothesized that PCT would increase ericaceous shrub competitive ability (such as ericaceous shrub cover, phenolic and condensed tannin concentrations, and rhizome growth), and that the increase from PCT would be more profound in maritime climates and on till soil deposits. We found PCT plots had higher ericaceous shrub cover at all site types and that PCT plots on till deposits had greater rhizome growth compared to control plots and sites on clay deposits, supporting our hypothesis. Additionally, till deposits arguably saw a decrease in N-mineralization under *Kalmia* compared to under *Pleurozium*, indicating stands with high ericaceous shrub cover on till deposits may experience reduced soil fertility. Although there was a lack of interactions between PCT and climate regime controlling ericaceous shrub responses, we noted the greater abundance of ericaceous shrubs found in the maritime climate and expect this region to have greater reductions to site fertility from ericaceous shrubs. Thus, PCT should be avoided in maritime climates on till deposits. It is expected that if a site continues to practice PCT during harvest cycles, the site quality would degrade. This is also supported by our study that found ericaceous shrub cover, current annual rhizome length, and condensed tannin and total phenolic concentrations increased with greater light availability. Immediately following PCT treatment, we would expect these variables to increase. If these variables increased over several harvest cycles, a stand that had high forest regeneration may experience a decline in site fertility to the point where conifers would experience “growth

check" from ericaceous species. We acknowledge the low replication of sites (n=4) within each site type and thus recommend that future studies increase the number of sites. Additionally, studies should be performed immediately following PCT treatment to verify our conclusions regarding ericaceous shrub responses to canopy openness. Many of the variables we measured were specifically from *Kalmia* due to previous studies that focused on *Kalmia* physiology, morphology, rhizome growth, and secondary phenols. Future studies should focus on other ericaceous species such as Labrador tea and *Vaccinium* spp. found within the Quebec boreal forest. Less information is known of these species in their role in competing with conifers as well as their competitiveness in differing climate regimes and soil deposits.

In Chapter 3 we hypothesized that scarification would decrease ericaceous shrub competitive ability (regarding the same variables as Chapter 2), and that the decrease would be more pronounced in continental climates. We found that scarification decreases the competitive ability of ericaceous shrubs but, contrary to our hypothesis, more so in a maritime climate. We found a greater decrease in total phenolic concentration, decrease in rhizome growth, and decrease in canopy openness on scarified plots compared to control plots in the maritime climate than in the continental climate. Additionally the trends in N-mineralization, the higher foliar N concentrations and lower foliar % N resorption on these same plots suggest a greater soil fertility compared to control plots in the maritime climate. This suggests scarification has a greater benefit in maritime climates than in continental climates for conifer growth. Shading ericaceous shrubs was achieved from planted conifer seedlings on control plots in the continental climate, reflecting a similar crown cover as scarified plots. However, to optimize conifer growth, scarification should continue to be practiced. We acknowledge that our study only included one site within each climate regime but believe that many of our conclusions can aid forest management with regional policies as well as for future studies. The multitude of interactions found between scarification and site controlling ericaceous shrub foliar and rhizomatous responses suggest that as the environment alters

from a maritime climate to a continental climate, we would expect ericaceous shrub responses to also change. Additionally, it would be beneficial to understand at which point regenerating conifer seedlings are free from growth check induced by ericaceous species. Therefore in order to map this gradient, multiple studies should be performed across Quebec as well as within each climate regime. In turn, these types of studies will aid in modeling forest growth and understanding the delay in forest growth due to ericaceous shrubs.

Currently ericaceous shrub species are considered problematic in terms of ericaceous shrub invasion after forest disturbances and therefore, are only considered during harvests and for forest regeneration. However ericaceous shrubs persist throughout the forest cycle and thus should be considered in forest management at all stages of a harvest cycle. If forestry practices that increase the risk of ericaceous shrub invasion, such as PCT, are continued with the expectation that scarification can alleviate issues caused by ericaceous shrubs, then productive sites will degrade in quality. Other measures would need to be taken such as fertilization (to improve nutrient availability) or manual removal of ericaceous shrubs. This is not in keeping with sustainable forestry views and would result in diminishing returns for forest management. The forest regime in Quebec has undergone previous reforms which gives evidence of the willingness of the MFFP and Chief Forester to adopt new management strategies based upon scientific findings. Therefore, it is our hope that the current forest management will consider our findings when making future management decisions and invest in future studies to further our knowledge of ericaceous species.

Ericaceous shrubs have the ability to determine plant growth by decreasing soil fertility and nutrient availability. This has the potential to influence the direction of forest succession in boreal forests worldwide. Thus, understanding understory responses and consequences to forest succession and regeneration is essential in maintaining productivity and the ecosystem. Additionally, examining ericaceous shrub species in differing climate regimes can inform

forest management on how ericaceous shrubs may respond to climate change. Forest management can, thus, use this information to calibrate forest growth simulation models under various climate change scenarios.

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